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Systematics of Megachiropteran Bats in the Solomon Islands

BY

CARLETON J. PHILLIPS

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INTRODUCTION

The Solomon Islands constitute an archipelago east of the large island of New Guinea and more than a thousand miles off the northeastern coast of Australia. This archipelago, which is principally of volcanic origin although sedimentary layers of calcareous rocks occur on many islands (Lever, 1934; Belkin, 1962), consists of a double chain of islands having a northwest-southeast axis of more than 600 miles. The archipelago is more or less an extension of New Guinea and in fact is connected to it in stepping-stone fashion by New Britain, New Ireland, and numerous smaller islands (see Fig. 1).

Australia and New Guinea have many kinds of mammals but the only terrestrial mammals in the Solomon Islands are a species of the genus *Phalanger* (order Marsupialia), and several species of four genera of rodents, one genus of which probably was introduced by man. Additionally, several kinds of bats have reached and colonized the Solomon Islands.

In the past 100 years at least 43 species and subspecies of Chiroptera of 16 genera have been recorded from the Solomon Islands; of these 27 species and subspecies of seven genera are in the suborder

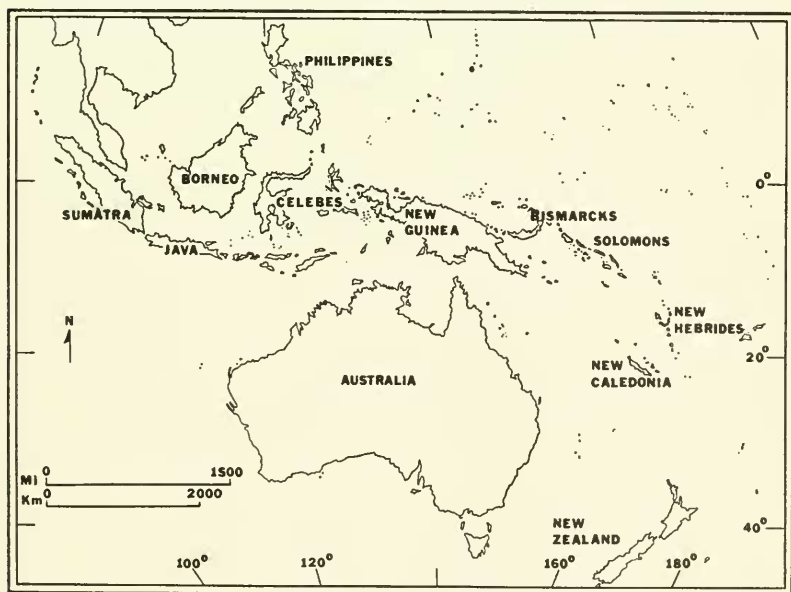


FIG. 1. Showing the Solomon Islands in relation to major adjacent land masses.

Megachiroptera. At least one genus of Megachiroptera is endemic as are numerous species of other genera, and subspecies of still other species.

In 1963 and 1964, the Bernice P. Bishop Museum sent several collecting parties to the British Solomon Islands Protectorate and the Australian Trust Territory of New Guinea. In the Solomons, J. Linsley Gressitt, Philip Temple, Peter Shanahan, and Ray Straatmann visited many of the larger and more accessible islands and collected a wealth of zoological materials. I have had the opportunity to study and report on specimens of mammals, especially bats, collected by the persons named and deposited in the Bishop Museum. This report is the third in a series on bats from the Solomons (Phillips, 1966; 1967). Other specimens, mostly obtained in 1944 by personnel of United States military units, are stored in the United States National Museum and have been available for study. Aims of the following report are to (1) identify the megachiropteran bats to species and subspecies and (2) discuss distribution of these bats in the Solomon Islands.

In all, 27 kinds (subspecies and monotypic species) of the order Megachiroptera are known from the Solomon Islands. These pertain to three subfamilies of the one family Pteropodidae.

The 43 Solomon Islands, having a total land area of more than 15,300 square miles (see Belkin, 1962:42-43), are listed in the gazetteer (see also Figure 2). Politically, all of the Solomon Islands except Buka and Bougainville, which are included in New Guinea Trust Territory under mandate to Australia, are in the British Solomon Islands Protectorate.

The Solomons are within 300 to 700 miles of the equator and have a fairly constant tropical climate, except at high elevations. The temperature varies little; monthly mean temperature is between 81° and 83° F. and at sea level ranges from about 70° to 93° F. yearly (Belkin, 1962:42).

Southeast tradewinds are relatively constant from May to October and this period, in general, is a dry season except at higher elevations on windward coasts. From December to March prevailing winds are from the north and precipitation throughout the island group is especially heavy. Rainfall on the island of Tulagi averages about 120 inches per year (Bryan, Edwin H., 1941; MS, p. 2, at Pacific Sci. Information Center, Bishop Museum) and up to 300 inches have been recorded on the north coast of Guadalcanal (Belkin, 1962:42-43). Occasional dry periods occur even in the period of December to March.

Most islands of the Solomon Group support dense tropical rain forest. Much of it has been modified by man. Some clearings and scattered coconut plantations are found along coasts. On some of the larger islands (for example, Guadalcanal) coastal scrub (especially on leeward coasts) and extensive grassy areas are to be found. Additional notes on vegetation are in the gazetteer.

The 165,000 persons living on the Solomon Islands are mostly Melanesians

but some are mixed Papuan, Malay, and Polynesian. These native peoples are notorious for their cannibalistic tendencies; the eating of human flesh usually was related to warfare, although malefactors and human sacrifices accounted for some of the cannibalism (Cranstone, 1961:29). Prior to the Second World War few Europeans visited the Solomons and several islands still remain beyond reach of modern-day technology. For example, Rennell and Bellona islands, south of the main part of the archipelago, are visited only rarely, and then only by a medical officer or the Resident Commissioner. According to Troughton (1936:341), the islanders in the interior of Bougainville as late as 1935, were prone to kill and feast upon strangers. In 1932, Lewis (1951:37) felt that the natives of Malaita Island were especially resistant to outside interference by Caucasians and reported that no "white man or foreigner" was safe on Malaita.

Troughton (1936), who listed Melanesian names for mammals, indicated that the native peoples distinguished between kinds of bats that closely resembled one another. Of these, the only bats that seem to be used as food belong to the genus *Pteropus*.

GAZETTEER

In the following list, currently-used names of islands are given; when available, older names and variant spellings are indicated in parentheses. For certain islands, especially those visited by field parties from the Bishop Museum or those frequently mentioned in previous literature on bats, some descriptive and ecological information also is provided.

Latitude and longitude of islands are from publication no. 881 of the Hydrographic Office of the United States Navy Department (Anonymous, 1944); names of islands were checked against a list by Brigham (1900); descriptive information mostly is from reports by Temple and Straatmann (1964, field notes, at the Department of Entomology, Bishop Museum).

ALU.—7°07' S, 155° 54' E.

BANIKA.—9° 05' S, 155° 13' E.

BARA (Gera).—9° 31' S, 160° 31' E.

BELLONA (Bello).—11° 18' S, 159° 48' E.

BOUGAINVILLE (Mamamolimo).—6° 12' S, 155° 15' E. This is the largest island in the Solomon Group, being 127 miles long (northwest to southeast) and about 59 miles across at the widest place. The highest elevations are 9850 and 10171 feet, at the tops of active volcanoes. Ecologically, Bougainville is mostly dense rain forest, which is less dense on the summits of higher mountains.

BUKA.—5° 15' S, 154° 38' E.

CHOISEUL.—7° 04' S, 157° 01' E. This island, formed along a northwest-southeast line of low mountains (maximum elevation of 3500 feet), is about 90 miles long and 20 miles wide. Most collecting was at Malangona (Sasamunga on some maps) on the southwestern coast.

FAURO.—6° 55' S, 156° 07' E. This small island, about 14 miles long (north-south) and six miles wide (east-west), lies about 10 miles south and east of Bougainville. Fauro is formed around a volcanic cone having a maximum elevation of 1925 feet; it has considerable dense mangrove swamp along the west coast, and mature rain forest with little understory growth. Most collecting was at Toumoua, on one of two southern peninsulas.

FLORIDA (Nggela).—9° 05' S, 160° 16' E. Florida, the main island in the Nggela Island Subgroup, is mountainous and except for some small grassy areas, supports dense rain forest. It is nearly 25 miles long (east-west) and

nine miles wide (north-south), with a maximum elevation, at Mount Barnett, of about 1366 feet. Most collecting was at Haleta, on the southwestern coast. At this locality there were scattered mangrove swamps, rain forest, and gardens inland.

GANONGGA (Ronogo, Ronongo).— $8^{\circ} 03' S, 156^{\circ} 35' E$.

GATUKAI.— $8^{\circ} 47' S, 158^{\circ} 12' E$.

GHIZO (Gizo, Keso).— $8^{\circ} 05' S, 156^{\circ} 59' E$.

GOWER (N'dai).— $7^{\circ} 54' S, 160^{\circ} 34' E$.

GUADALCANAL (Guadalcanar).— $9^{\circ} 15' S, 159^{\circ} 35' E$. Guadalcanal is mostly of volcanic origin and has an irregular chain of mountains along the southern coast. The highest elevation is 8005 feet at Mount Popomanasiu. This large island is nearly 80 miles long (east-west) and 25 miles wide (north-south). Most of the northwestern part of Guadalcanal supports *alang-alang* grass. The remainder of the island is heavily wooded.

KILINAILAU (Cartaret).— $4^{\circ} 44' S, 155^{\circ} 28' E$.

KOLOMBANGARA (Duki, Kulambangara).— $8^{\circ} 00' S, 157^{\circ} 05' E$. Kolombangara, formed from an extinct volcano, is about 18 miles in diameter and nearly circular. The highest peaks, rising as precipitous cliffs in some places, reach a maximum elevation of about 5000 feet. The vegetation is mostly virgin rain forest. Mangrove swamp and small coconut groves occur along the coast. Field parties from the Bishop Museum were able to reach the highest elevations, and concentrated their work along the southwestern side of the island.

MALAITA (Mala, Malanta, Malayta).— $9^{\circ} 00' S, 161^{\circ} 00' E$. This long (104 miles northwest to southeast), narrow (about 23 miles at its widest spot) island, between Santa Ysabel and San Cristobal islands, is basically of volcanic origin with some limestone (coral) deposits along the coast. Mount Kolovrat,

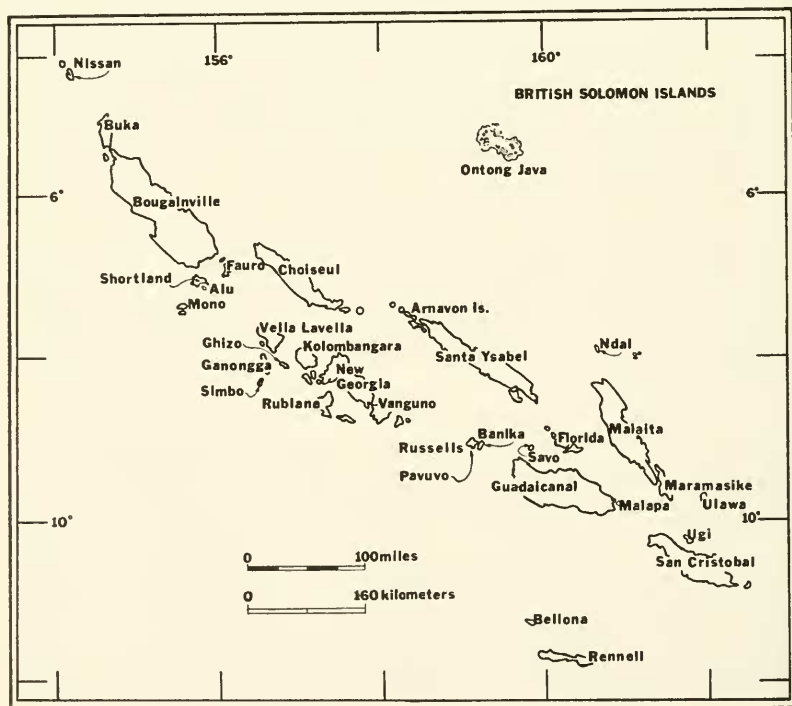


FIG. 2. Solomon Islands. Principal islands are named.

having an elevation of 4275 feet, is the highest point. The Bishop Museum field party lived at Dala, in dense rain forest about 12 miles north of Auki on the northwestern coast of Malaita.

MALAPA.—9° 49' S, 160° 53' E.

MONO (Treasury).—7° 22' S, 155° 35' E. This is a small island (maximum elevation 1150 feet) in the Treasury Island Subgroup just south of Bougainville. Mono is about nine miles long (east-west) and five and one half miles wide (north-south). The basic volcanic core is described in field notes as topped with coral limestone.

NEW GEORGIA (Kausagi).—8° 20' S, 157° 30' E. The New Georgia Subgroup is composed of 11 moderate-sized islands and islets. New Georgia Island, the main member of the subgroup, is 50 miles long (northwest to southeast) and from five to 30 miles wide. On the northern side several volcanic peaks attain an elevation of about 3000 feet. The entire island is forested.

NGGELA (Florida Islands).—4° 31' S, 154° 11' E. This subgroup consists of several small to medium-sized islands between Guadalcanal and Malaita. Florida is the main island.

NISSAN (Green, Sir Charles Hardy's).—4° 31' S, 154° 11' E.

NUKUMANU (Le Maira, Tasman).—4° 32' S, 159° 25' E.

ONTONG JAVA (Lord Howe Atoll, Liuinuwu).—5° 25' S, 159° 30' E.

PAVUVO.—9° 04' S, 159° 08' E.

RAMOS.—8° 16' S, 160° 11' E.

RENNELL.—11° 38' S, 160° 14' E. This island, of limestone (coral) origin, along with Bellona, is nearly 100 miles southwest of any other member of the Solomons and has been regarded, because of this distance, as an oceanic island instead of a continental island. It is about 50 miles long (east-west) and nine miles wide (north-south); its highest elevation is 500 feet.

ROVIANA (Rendova, Rovianna, Rubiana).—8° 21' S, 157° 20' E.

RUSSELL.—9° 04' S, 159° 12' E.

SAN CRISTOBAL (San Christoval, Bauro, Makira, Arussi).—11° 33' S, 161° 43' E. This island is composed mostly of ancient volcanic rock, has a maximum elevation of 4100 feet, is nearly 70 miles long (northwest to southeast) and 24 miles wide, and supports a dense rain forest.

SANTA YSABEL (George, Ysabel, San Isabel, Isbel, Mahaga).—8° 00' S, 159° 07' E. Santa Ysabel is a long (90 miles from northwest to southeast), narrow (19 miles at the widest spot), forested island, consisting of a single chain of volcanic mountains. The numerous bays and mouths of rivers provide excellent anchorages. Collecting was at Tatamba approximately two miles south of Tanambuli where the considerable area of forest was dense and bamboo thickets were abundant.

SAVO (Savu).—9° 08' S, 159° 49' E.

SHORTLAND.—7° 03' S, 155° 47' E.

SIKAIANA (Stewart).—8° 22' S, 162° 44' E.

SIMBO (Narovo, Naorovo, Naravo, Navoro, Sembo).—8° 16' S, 156° 31' E.

STIRLING.—7° 25' S, 155° 35' E.

TANABULI (Tanambuli, Tunnibili, Tunnibilis, Tunnibul, Tunnivula).—8° 24' S, 159° 35' E.

TAUU (Marqueen, Mortlock).—4° 48' S, 157° 32' E.

TELIPARI.—8° 15' S, 157° 32' E.

UGI.—10° 14' S, 161° 44' E.

VANGUNO (Vangunu).—8° 39' S, 158° 00' E.

VELLA LAVELLA.—7° 43' S, 156° 40' E. The coastline is rugged and indented by numerous small bays. Some peaks are 3000 feet high. The southeastern half of Vella Lavella is said to consist of uplifted coral, and to be thickly planted to coconut palms. The native population is concentrated here.

The northwestern half of the island is rain forest and is nearly uninhabited. Most of the collecting was at Pusiasama, on the southern beach and on Ulo Crater, an extinct volcano at the middle of the island.

YANNTA.—10° 20' S, 161° 20' E.

METHODS AND MATERIALS

The phylogenetic arrangement and nomenclature in the text beyond are mainly that of Laurie and Hill (1954). The synonymies for accounts of genera are as follows: (1) first use of the generic name employed along with the original description, and (2) original proposals, in chronological order, of other generic names subsequently applied to the bat in the Solomons. The synonymies in accounts of species and subspecies are as follows: (1) first use of the accepted name, followed by its type locality, followed, in chronological order, by other references to the first name-combination, (2) first use of the name-combination employed herein (if different from the original combination), followed, in chronological order, by other references to the present name-combination, and (3) other name-combinations, in chronological order, employed for the bat in the Solomons. The word "part" is used in parentheses after a name if some specimens listed under that name are from the Solomon Islands and are referable to the species or subspecies being written about.

Unless noted otherwise, specimens listed as examined were prepared originally as museum skins with skulls. Approximately 70 per cent of bats collected in the Solomons were preserved in formalin and now are stored in alcohol. Because it was necessary to obtain dimensions and examine various morphological characteristics of skulls, many crania were extracted from bats preserved in alcohol.

Although all specimens in the Bishop Museum from the Solomon Islands have been catalogued with the prefix BBM-BSIP, catalogue numbers without prefixes in the lists of specimens examined refer to this museum. Catalogue numbers with the prefix USNM refer to specimens in the U. S. National Museum and those with the prefix AM-M refer to specimens in the Australian Museum.

Unless indicated otherwise, all measurements in this paper are in millimeters and are of adults. Cranial measurements, and external measurements of specimens stored in alcohol, were taken by me. The cranial measurements were taken with dial calipers using techniques described by Hall (1946:672-685). External measurements (except length of forearm) of specimens originally prepared as dried study skins, were transcribed from specimen labels.

Capitalized color nomenclature is from Ridgway (1912). Noncapitalized color terms are from published reports that did not use Ridgway's terminology.

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reviewed the manuscript. Other persons who have given me assistance and, in some cases, arranged for loans of comparative materials, are: Dr. David H. Johnson, Division of Mammals, United States National Museum; Mr. Hobart M. Van Deusen and Dr. Richard G. Van Gelder, Archbold Expeditions and Department of Mammalogy, American Museum of Natural History; Messrs. Ellis LeG. Troughton and Basil Marlow, Mammal Department, The Australian Museum; Dr. Joseph Curtis Moore, Department of Mammalogy, Field Museum of Natural History; Mr. John Edwards Hill, Mammal Room, British Museum (Natural History); Prof. William B. Davis, Department of Zoology, Texas A & M University; Miss Barbara Lawrence, Museum of Comparative Zoology, Harvard University. Messrs. Jerry R. Choate and H. H. Genoways, two colleagues in zoology at The University of Kansas, have assisted me in many ways, for which I am grateful. Linda Anne Phillips, my wife, prepared many of the figures and tables used herein. I thank also Setsuko Nakata, Edwin H. Bryan, Robert Bowan, and Ilse Koehler, who, as staff members of the Bishop Museum, were especially helpful to me. Most of the specimens reported herein were collected by Philip Temple and Peter Shanahan.

Key to Genera

1. Uropatagium lacking, or, if present, deeply indented in center; tail vertebrae absent, or if present, free. 2
- 1'. Uropatagium present, not indented; tail vertebrae present, free or in uropatagium. MICROCHIROPTERA 1
- 2(1). External tail-vertebrae lacking, or, if present, less than 3 mm long. . . 3
- 2'. External tail-vertebrae more than 3 mm long. 6
- 3(2). Small or medium-sized (forearm less than 50); tongue long, extensible. 4
- 3'. Large (forearm more than 80); tongue not long and extensible. 5
- 4(3). Uropatagium present; small claw present on second phalanx of second digit; tail short (about 3 mm). **Macroglossus**, p. 812
- 4'. Uropatagium absent; no claw on second phalanx of second digit; no tail. **Melonycteris**, p. 814
- 5(3'). Entire back set with hair; wing membranes not meeting at middle of back. **Pteropus**, p. 793
- 5'. Back naked; wing membranes meeting at middle of back,
Pteralopex, p. 790
- 6(2'). Nostrils having definite tubelike extensions. **Nyctimene**, p. 817
- 6'. Nostrils lacking tubelike extensions. 7
- 7(6'). Forearm less than 80; large, sharp claw on second phalanx of second digit; four upper incisors. **Rousettus**, p. 787
- 7'. Forearm more than 90; small, blunt claw on second phalanx of second digit; two upper incisors. **Dobsonia**, p. 807

Family PTEROPODIDAE

Subfamily Pteropodinae

Rousettus Gray

1821. *Rousettus* Gray, London Medical Repository, 15:299, April 1.
 1843. *Xantharpyia* Gray, List of species . . . British Museum, p. 37.
 1852. *Cynonycteris* Peters, Reise nach Mossambique, p. 25.

The genus *Rousettus* occurs throughout the tropical regions of the Old World, and in the Solomons is readily distinguished from all other megachiropteran genera by having both a small claw on the second digit and free caudal vertebrae. The oriental species have been divided into two groups on the basis of size (Tate, 1942:344). The subspecies *Rousettus amplexicaudatus hedigeri* appears to be the sole representative of this genus in the Solomon

Islands. Prior to 1953, several workers (Thomas, 1887b:323, 1888b:475; Matschie, 1899:68; Sanborn, 1931:11) used the name *Rousettus amplexicaudatus brachyotis* for it, but Pohle (1953) suggested that the specimens from the Solomons recorded by earlier workers were *R. a. hedigeri* named by him on the basis of the specimen that he saw from Bougainville.

Rousettus amplexicaudatus

Rousettus amplexicaudatus has at least three subspecies, one of which is endemic to the Solomon Islands. The species is wide-ranging, being known from as far west as Thailand (Ellerman and Morrison-Scott, 1966:93) and as far east as the Solomons.

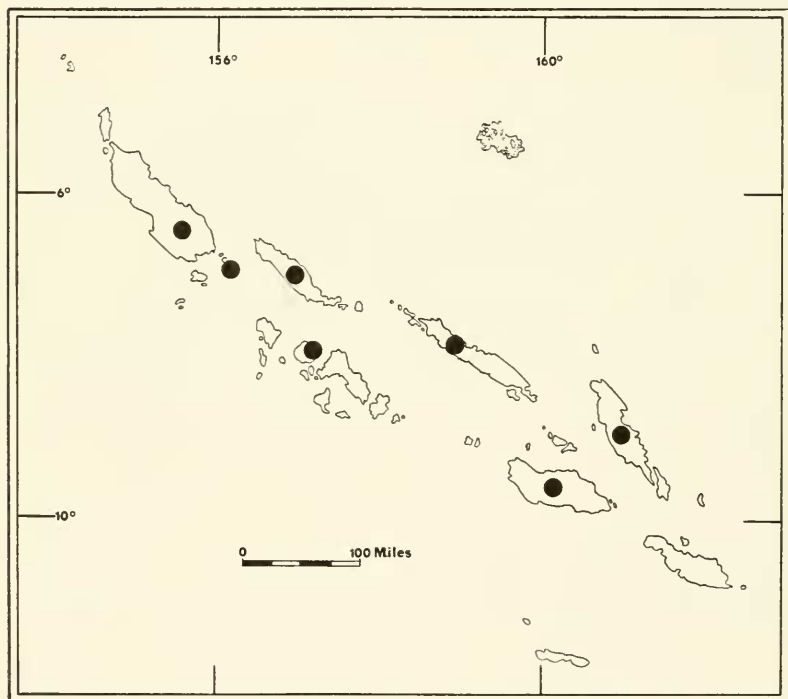


FIG. 3. Distribution of *Rousettus amplexicaudatus hedigeri*. For names of islands see Fig. 2.

Rousettus amplexicaudatus hedigeri Pohle

1953. *Rousettus amplexicaudatus hedigeri* Pohle, Z. Säugetierk., 17:127, October 27, type from Bougainville.
1887. *Cynonycteris brachyotis*, Thomas, Proc. Zool. Soc. London, p. 323, March 15; 1888, Thomas, Proc. Zool. Soc. London, p. 475, December 4, from Fauro.
1889. *Xantharpyia brachyotis*, Matschie, Die Megachiroptera . . . naturkunde, p. 68, from Guadalcanal.

1912. *Rousettus brachyotis*, Andersen, Catalogue of the Chiroptera
British Museum, 1:809; 1931, Sanborn, Publ. Field Mus. Nat. Hist.,
Zool. Ser., 18:11, February 12, from Santa Ysabel.

Specimens examined (20 males and 21 females; all in alcohol; ten crania extracted and cleaned).—Guadalcanal in May, 23863, 23915; Fauro in April, 23804-5; Malaita in June, 24079; Choiseul in March, 23563-4, 23616, 23627, 23630, 23632-3, 23642, 23658, 23663-4, 23680, 23692-3, 23713, 23722; Kolombangara in January and February, 23343, 23366, 23382-4, 23389-90, 23408-9, 23424, 23455, 23471-4, 23501.

Measurements.—Average and extreme external measurements of 13 males and 18 females are, respectively, as follows: Length of head and body, 104.4 (99-118), 108.6 (104-117); tail vertebrae, 16.8 (13-19), 17.6 (15-24); hind foot, 18.0 (16-19), 16.2 (12-18); ear, 15.9 (15-17), 15.0 (14-16); length of forearm, 70.1 (66.0-74.1), 68.1 (65.0-69.1). Average and extreme measurements of skulls of five males and five females are, respectively, as follows: Greatest length of skull, 33.2 (33.0-33.7), 31.5 (30.9-32.1); condylobasal length, 31.3 (30.9-31.9), 30.1 (29.3-30.8); palatal length, 14.0 (13.3-14.8), 13.3 (13.0-13.7); zygomatic breadth, 20.8 (19.8-21.8), 19.4 (18.7-20.8); length of maxillary tooth-row, 11.0 (10.9-11.3), 10.3 (10.1-10.6); length of mandibular tooth-row, 12.6 (12.4-12.9), 11.8 (11.7-12.2).

Remarks.—The specimens from Choiseul, Kolombangara, and Malaita islands provide new records of distribution for *Rousettus amplexicaudatus hedigeri* (Fig. 3). It was described as smaller than *R. a. brachyotis* Dobson, which is known from New Guinea, Amboina, and the Bismarck Archipelago (Pohle, 1953:127-128). Andersen (1912:809) gave the range of length of forearm in *R. a. brachyotis* as 73-81, whereas Pohle (1953:127) gave the length of forearm of the type specimen of *R. a. hedigeri* (adult male) as 67. Measurements of specimens examined by me indicate that *hedigeri* occurs throughout the Solomon Islands. Cranial measurements of my specimens and Pohle's type are less than those of *R. a. brachyotis* (see Andersen, 1912:48).

Sanborn (1931:11) noted that the forearms of three males examined by him were longer than that of a female. Mean and range for length of forearm of males and females listed herein, respectively, are 70.1 (66.0-74.1) and 68.1 (65.0-69.1). Also, each of seven cranial measurements taken by me averaged more in males than in females. Sagittal and lambdoidal crests are more prominent in males than in females.

As shown in Table 1, adult females obtained in December and January were lactating when captured whereas those obtained in March, April, and

TABLE 1. A Summary of Breeding Data for Females of *Rousettus amplexicaudatus hedigeri* Collected December to June.

MONTH	Total number collected	Number adult ♀♀ collected	Number lactating	Number of immature individuals
December	3	3	3	0
January	11	11	8	0
February	6	0	..	1
March	16	1	0	9
April	2	2	0	0
June	1	1	0	0

June were not. More than half of the individuals collected in March were immature (judging from small size, unfused epiphyses, and lack of wear on teeth). The immature individuals probably had been nursing in December and January.

Pteralopex Thomas

1888. *Pteralopex* Thomas, Ann. Mag. Nat. Hist., ser. 6, 1:155, February 1.
1762. *Pteropus* Brisson, Regnum animale . . . , ed. 2, p. 153.

Pteralopex, with one species and two subspecies, is the only megachiropteran genus endemic to the Solomons. Thomas (1888b:475) considered this unusual bat a relic, isolated from the time when pteropodids had cuspidate cheek-teeth. Although two workers (Matschie, 1899:11; Simpson, 1945:54) have synonymized *Pteralopex* with *Pteropus*, I regard *Pteralopex* as a morphologically distinct genus.

Individuals of *Pteralopex* can be distinguished from all species of *Pteropus* in the Solomon Islands by the following features: wing membranes originate along dorsal midline; braincase diminutive relative to rest of skull; sagittal crest pronounced; cheek-teeth cuspidate, broad and massive; i_2 about 10 times larger than i_1 ; upper canines with well-developed secondary cusp; postorbital process fused with zygomatic arch, forming complete bony ring around orbit.

Andersen (1909a:216; 1912:436) considered the relationships of *Pteralopex* and *Pteropus* and concluded that *Pteropus pselaphon* Lay, 1829, from the Sulphur Islands east of Taiwan, and *Pteropus samoensis* Peale, 1848, from the Samoan Islands, were the "closest" living relatives of *Pteralopex*. He stated further that *Pteralopex* "presents in fact scarcely a single character which is not either developed to a certain extent or at least distinctly foreshadowed in *Pteropus pselaphon*, *pilosus*, *tuberculatus*, or *leucopterus*." In summary, Andersen thought several species of *Pteropus* had undergone evolutionary development resembling that in *Pteralopex*, and that the latter, with its massive, cuspidate cheek-teeth, could be considered a highly modified *Pteropus*. For this hypothesis to be plausible, one must assume that the originally complex cheek-teeth of pteropodids became simple and, at least in the case of *Pteralopex*, secondarily became complex once again. According to present-day theory of evolutionary development, his hypothesis is improbable. Thomas (1888b:475) probably was correct when he considered *Pteralopex* an isolated relic.

Although *Pteralopex* usually is listed after *Pteropus* in phylogenetic arrangements (see, for example, Sanborn, 1931:21; Pohle, 1953:129; Laurie and Hill, 1954:40), I have placed *Pteralopex* before *Pteropus*.

Pteralopex atrata

Two subspecies of *Pteralopex atrata* (*P. a. atrata* and *P. a. anceps*) have been named; specimens of both are rare in museum collections. Thomas (1888a: 155) described adults of *atrata*. Sanborn (1931:21) examined the one additional specimen known to me and reported that it agreed with Thomas' description.

Andersen (1909b:266) used a subadult female ("nearly fully grown") as the holotype of *anceps*. At least five additional specimens, all adults, of *anceps* now are housed in various collections. Judging from these individuals,

the holotype of *anceps* was only four-fifths grown and because he used an immature individual, Andersen's (1912:437) criteria for distinguishing the two subspecies mostly are invalid.

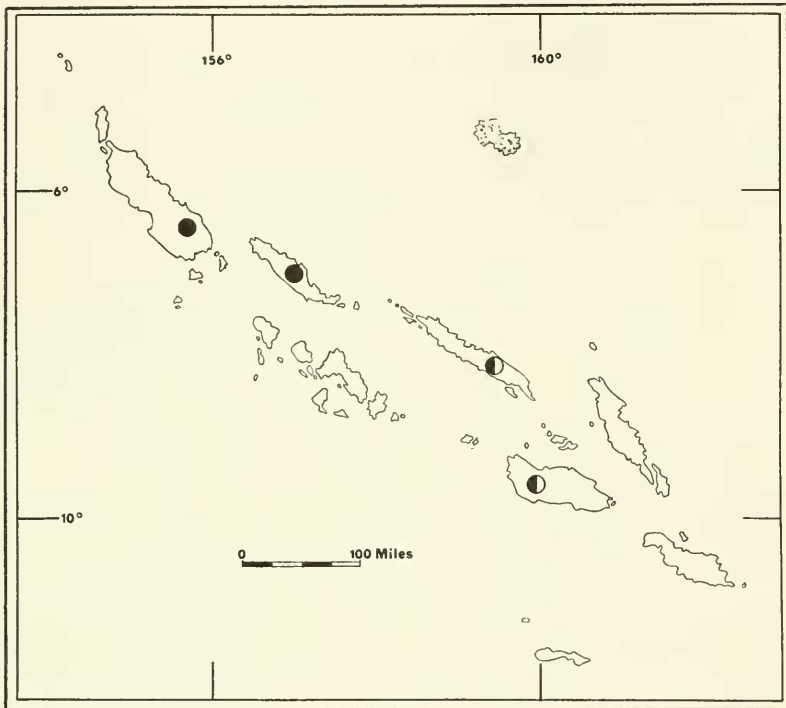


FIG. 4. Distribution of *Pteralopex atrata*; *P. atrata atrata* (◐) and *P. atrata anceps* (●). For names of islands see Fig. 2.

Key to Subspecies of *Pteralopex atrata*

1. Length of forearm 139-144 mm.; dorsal surface of distal one-fourth of tibia and entire metatarsus naked; known only from Guadalcanal and Santa Ysabel islands. *Pteralopex atrata atrata*
- 1'. Length of forearm 162-166 mm.; dorsal surface of distal one-fourth of tibia and entire metatarsus furred; known only from Bougainville and Choiseul islands. *Pteralopex atrata anceps*

Pteralopex atrata atrata Thomas

1888. *Pteralopex atrata* Thomas, Ann. Mag. Nat. Hist., ser. 6, 1:155, February, type from Guadalcanal; 1888, Thomas, Proc. Zool. Soc. London, p. 475, December 4; 1896, Heude, Mém. Hist. Nat. Emp. China, 3:179; 1897, Trouessart, Catalogus Mammalium, 1:83; 1907, Miller, Bull. U. S. Nat. Mus., 57:60, June 29; 1912, Andersen, Catalogue of the Chiroptera British Museum, 1:439; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:21, February 12, from Santa Ysabel.

1954. *Pteralopex atrata atrata*, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 40, June 30.
1899. *Pteropus (Pteralopex) atrata*, Matschie, Die Megachiroptera . . . naturkunde, p. 11; 1904, Trouessart, Catalogus Mammalium . . ., Suppl., p. 49.

Specimens examined.—None.

Remarks.—*Pteralopex atrata atrata* is known from four specimens from Guadalcanal and one from Santa Ysabel (Sanborn, 1931:21).

Sanborn (*loc. cit.*) reported that a specimen wounded at night, while feeding on young green coconuts, was the only fruit bat that attempted to attack the collectors. Troughton (1936:348) has suggested, on the basis of his experiences with *Pteropus*, that this behavior probably was a reaction from fear rather than an indication of general aggressiveness on the part of *Pteralopex*.

Pteralopex atrata anceps Andersen

1909. *Pteralopex anceps* Andersen, Ann. Mag. Nat. Hist., ser. 8, 3:266, March, type from Bougainville; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:437; 1936, Troughton, Rec. Australian Mus., 14:348, April 7; 1953, Pohle, Z. Säugetierk., 17:129, October 27.
1954. *Pteralopex atrata anceps*, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 40, June 30.

Specimens examined (three males, two females; one skull-only and one in alcohol).—Choiseul in March, 23682; Bougainville in July, USNM 276973-74, USNM 276928, USNM 277112.

Measurements.—Measurements of three males and one female are, respectively, as follows: Length of head and body, 280, 271, 261, 255; hind foot, 50, 54, 52, 59; ear, 23, 23, 26, 22; length of forearm, 160, 162, 166, 171; greatest length of skull, 77.6, 77.9, 78.9, 77.0; condylobasal length, 74.3, 74.3, 75.5, 73.8; zygomatic breadth, 42.2, 45.4, 43.1, 42.6; breadth across upper canines, 18.7, 21.1, 19.0, 19.0; breadth across first upper molars, 22.2, 25.3, 22.9, 22.0; length of maxillary tooth-row, 29.3, 29.8, 28.9, 28.2; length of mandibular tooth-row, 32.8, 32.8, 32.1, 31.4.

Remarks.—Heretofore, *Pteralopex atrata anceps* was not known from Choiseul. The specimen from that island agrees well with specimens in the U. S. National Museum from Cape Torokina, Bougainville.

The type specimen of this subspecies is a subadult and is smaller than the specimens examined by me; Andersen (1912:440) gave length of forearm of the type as 137 (as opposed to 164 in adults). He (1912:438) figured the dentition of *anceps* and described the ways in which it differed from the dentition of *atrata*. Although he (1912:437) concluded that *anceps* and *atrata* represented "two stages of specialization of . . . dentition," there apparently are few, if any, dental differences between the two subspecies. Teeth of adults of *anceps* differ from teeth of the immature type of *anceps* as follows: in adults the anterior basal ledge of P4 extends onto the labial surface, whereas in the type it does not; and maxillary and mandibular teeth in adults are spaced as in the subspecies *atrata* (see Andersen, 1912:438, fig. 22) and not crowded as in the type of *anceps*. Distance between individual cheek-teeth apparently increases with growth of the cranium and mandible.

Adults of *P. a. anceps* that I examined are darker than the subadult type. The mantle in these adults is black, whereas it is seal-brown in the type (Andersen, 1912:439).

An adult female was lactating when obtained on Bougainville in July (USNM 276928).

Pteropus Brisson

1762. *Pteropus* Brisson, Regnum animale . . . , ed. 2, p. 153.

Remarks.—More species (seven) and subspecies (12) of *Pteropus* occur in the Solomon Islands than of any other chiropteran genus. Other kinds of *Pteropus*, as yet unknown, may live there.

The relationships among the species of these large fruit-eating bats, com-

Key to *Pteropus* in the Solomon Islands

1. Premolars having distinct basal ledges; molars 2.5-4.0 wide. 2
- 1'. Premolars lacking definite basal ledges; molars 1.0-2.4 wide. 14
- 2(1). Rostrum unshortened (orbit to anterior tip of nasals about one-third greatest length of skull); dorsal surface of tibiae nearly naked. 3
- 2'. Rostrum shortened (orbit to anterior tip of nasals less than one-third greatest length of skull); dorsal surface of tibiae usually at least partially furred. 8
- 3(2). Forearm more than 128. 4
- 3'. Forearm less than 128. 5
- 4(3). Forearm about 155; venter and dorsum nearly black, mantle pale yellow. *P. tonganus geddiei*, p. 798
- 4'. Forearm 128-136; venter and dorsum near Mars Brown, mantle Ochraceous or Cream-Buff. *P. hypomelanus luteus*, p. 796
- 5(3'). Mantle dark, russet or cinnamon, not strongly contrasting with color of back. *P. admiralitatum solomonis*, p. 796
- 5'. Mantle pale, Ochraceous-Buff or Cream-Buff, strongly contrasting with color of back. 6
- 6(5'). Mantle Ochraceous-Orange to Ochraceous-Buff, hairs pale basally; forearm 108-111. *P. admiralitatum goweri*, p. 797
- 6'. Mantle Ochraceous to Cream-Buff, but hairs dark brown basally; forearm 110-122. 7
- 7(6'). Length of forearm 110-112. *P. admiralitatum colonus*, p. 796
- 7'. Length of forearm about 122. *P. howensis*, p. 797
- 8(2'). Forearm more than 145. 9
- 8'. Forearm less than 144. 12
- 9(8). Forearm more than 162. 10
- 9'. Forearm less than 162. 11
- 10(9). Forearm 167-173. *P. rayneri grandis*, p. 801
- 10'. Forearm about 164. *P. rayneri rubianus*, p. 802
- 11(9'). Flanks and lower belly brightly colored, Burnt Sienna to Sanford's Brown; forearm less than 150. *P. rayneri monoensis*, p. 803
- 11'. Flanks and lower belly darker, near tawny; forearm more than 150, *P. rayneri lavellanus*, p. 802
- 12(8'). Pelage of dorsum tricolored; rump brightly colored; forearm 139-141, *P. rayneri rayneri*, p. 800
- 12'. Pelage of dorsum bicolored; rump dark; forearm less than 135. 13
- 13(12'). Mantle tawny with some Ochraceous-Buff; forearm about 130, *P. rayneri renelli*, p. 804
- 13'. Mantle russet, lacking Ochraceous-Buff; forearm about 121, *P. rayneri cognatus*, p. 803
- 14(1'). Forearm more than 131; dorsum Tawny Olive. *P. mahaganus*, p. 806
- 14'. Forearm less than 100; dorsum dark brown. *P. woodfordi*, p. 804

monly termed "flying foxes," are obscure and the genus is in need of revision. The basic, definitive work is still that of Andersen (1912). Tate (1942) and Felten (1964a, 1964b) have offered some additional remarks but groupings and suggested relationships of species of *Pteropus* almost entirely are the products of Kund Andersen. According to present-day concepts of variation and speciation, Andersen's criteria are artificial.

Basically, there are three "species-groups" of *Pteropus* in the Solomon Islands. The first is composed of species in which the rostrum is "unshortened" (its length about one third of greatest length of skull), and the cheek-teeth are of moderate size (M1 is 2.8—3.2 wide). The species are *P. hypomelanus*, *P. admiralitatum*, *P. tonganus*, and *P. howensis*. The first and second species were placed in the *Pteropus hypomelanus* group by Andersen (1912:98).

In the second group the rostrum is "shortened" (its length less than one third of greatest length of skull) and the cheek-teeth are of moderate to large size (M1 3.3-4.1 wide). *Pteropus rayneri*, endemic to the Solomons and represented there by at least seven subspecies, fits into this category.

The third group is represented by *P. mahaganus* and *P. woodfordi*. Both species are endemic to the Solomon Islands. In these species the rostrum is unshortened but the cheek-teeth are greatly reduced, especially in width (M1 is 1.0—2.2 wide). Both *P. mahaganus* and *P. woodfordi* can be included in the *Pteropus scapulatus* group of Andersen (1912:402).

Pteropus hypomelanus

Pteropus hypomelanus is a wide-ranging species of flying fox having at least seven subspecies; three occur in southeastern Asia, two on and near Celebes, and two in New Guinea and islands adjacent to the southeastern coast of New Guinea, including one island in the Solomons (Ellerman and Morrison-Scott, 1966:95; Laurie and Hill, 1954:32-33).

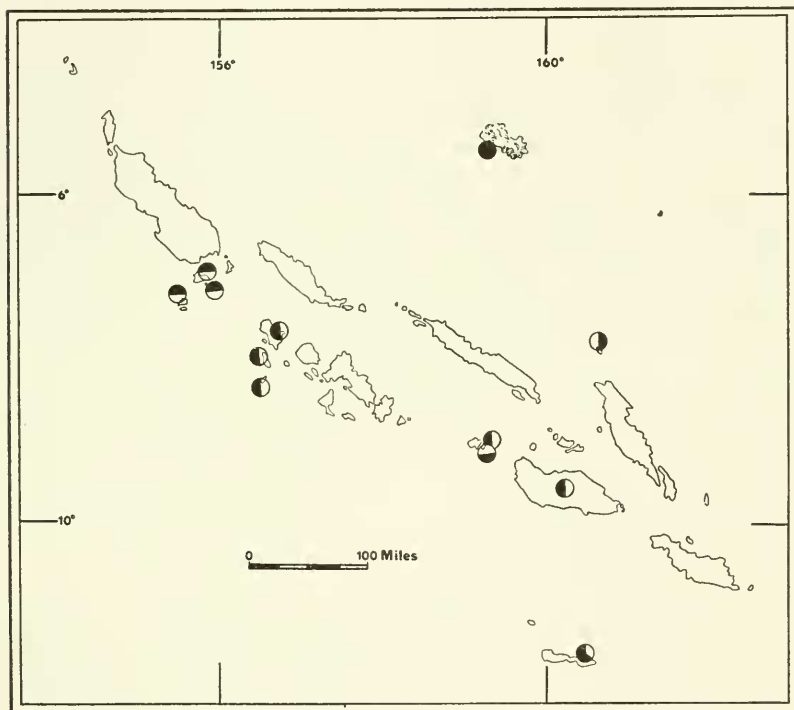


FIG. 5. Distribution of *Pteropus hypomelanus luteus* (◐), *Pteropus admiraltatum solomonis* (◑), *Pteropus a. colonus* (◒), *Pteropus a. goweri* (◓), *Pteropus tonganus geddiei* (◔), and *Pteropus howensis* (●). For names of islands see Fig. 2.

Pteropus hypomelanus luteus Andersen

1908. *Pteropus hypomelanus luteus* Andersen, Ann. Mag. Nat. Hist., ser. 8, 2:362, October, type from Kiriwini Island, Trobriand Islands; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:128; 1947, Sanborn and Beecher, Jour. Mamm., 28:388, November 19, from Banika Island, Russell Islands.

Specimens examined.—None.

Remarks.—Andersen (1908:362) identified specimens of *Pteropus hypomelanus* from eastern New Guinea and three nearby islands (Conflict Islands, Trobriand Islands, and Woodlark Island) as *P. hypomelanus luteus*. Sanborn and Beecher (1947:388) identified a female from Banika Island in the Solomons as of this subspecies although this specimen was darker and had a slightly smaller skull than typical *P. hypomelanus luteus*. They noted that the pelage of the venter of the female was uniformly dark rather than the typical Ochraceous-Buff to Cream-Buff; the specimen was regarded as a dark phase of the subspecies. Although not recorded previously for *luteus*, other subspecies of *P. hypomelanus* were known in dark phase as well as pale and intermediate phases of coloration (Andersen, 1912:122). The reported occurrence of *P. h. luteus* on Banika Island extended the known geographic range about 450 miles eastward from Woodlark Island.

Pteropus admiralitatum

Three subspecies, all about the same size but differing in coloration, have been described from the Solomon Islands. *P. a. goweri* is known only from Gower (Ndai) Island, notably removed from the western chain of islands inhabited by *P. a. colonus* and *P. a. solomonis*. Only one other subspecies, from the Admiralty Islands, is known.

Pteropus admiralitatum solomonis Thomas

1904. *Pteropus solomonis* Thomas, Novit. Zool., 11:597, type from Ghizo Island; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:149; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:12, February 12, from Ronongo (Ganongga), Vella Lavella, and Narovo (Simbo) islands; 1947, Sanborn and Beecher, Jour. Mamm., 28:389, November 19, from Banika and Guadalcanal islands.
1954. *Pteropus admiralitatum solomonis*, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 33, June 30.

Specimens examined.—None.

Remarks.—Andersen (1912:149) considered *Pteropus admiralitatum*, and especially the subspecies *P. a. solomonis*, to be the easternmost "representative" of *Pteropus hypomelanus*. In comparison with *P. hypomelanus luteus*, *P. a. solomonis* differs mostly in size, being much smaller (length of forearm about 110 rather than 134). It is now known that both species occur on Banika Island in the Solomons.

The subspecies *P. a. solomonis* has been recorded from a "chain" of islands that included Vella Lavella, Simbo, Ghizo, Ganongga, Banika, and Guadalcanal (see Fig. 5).

Pteropus admiralitatum colonus Andersen

1908. *Pteropus colonus* Andersen, Ann. Mag. Nat. Hist., ser. 8, 2:363, October, type from Shortland Island; 1912, Andersen, Catalogue of

the Chiroptera . . . British Museum, 1:150; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:12, February 12, from Mono Island.

1954. *Pteropus admiralitatum colonus*, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 33, June 30.
1887. *Pteropus hypomelanus* (part), Thomas, Proc. Zool. Soc. London, p. 471, December 4; 1898, Trouessart, Catalogus Mammalium . . ., 1:82, from "I. Salomonis."
1899. *Pteropus (Spectrum) hypomelanus* (part), Matschie, Die Megachiroptera . . . naturkunde, p. 24.

Specimens examined.—None.

Remarks.—*Pteropus admiralitatum colonus* is the largest of the three subspecies that occur in the Solomon Islands. It closely resembles *P. hypomelanus luteus*, except in being smaller throughout (see Andersen, 1912:151-152, for measurements) and darker on the underparts.

This bat has been found in a group of small islands (Alu, Mono, and Shortland) about 30 miles south of Bougainville. Because of this proximity and because yet another subspecies of this species occurs northward of Bougainville, it is interesting that neither Troughton (1936) nor Pohle (1953) included the species in their faunal lists for Bougainville.

Andersen (1912:152) indicated that the M1 in *P. admiralitatum colonus* is smaller than in *P. a. solomonis*, the subspecies found in islands to the southeast (4.4-4.5 and 5.2, respectively), but Sanborn (1931:13) studied specimens of these two subspecies that overlapped in size of M1.

Pteropus admiralitatum goweri Tate

1934. *Pteropus goweri* Tate, Amer. Mus. Novit., 718:1, May 4, type from Gower (Ndai) Island.
1954. *Pteropus admiralitatum goweri*, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 33, June 30.

Specimens examined.—None.

Remarks.—*Pteropus admiralitatum goweri* was described from six specimens collected in 1930 by the Whitney South Sea Expedition (Tate, 1934:1). This subspecies closely resembles the other two subspecies of *P. admiralitatum* (*colonus* and *solomonis*) found in the Solomon Islands. Color and length of forearm (see key on p. 793) seem to be the only reliable criteria for distinguishing between these subspecies. The longitude of Gower Island, 160° 34' E, was incorrectly listed in Laurie and Hill (1954:152) as 159° 34' E.

Pteropus howensis Troughton

1931. *Pteropus howensis* Troughton, Proc. Linn. Soc. New South Wales, 56:204, June 24, type from Lord Howe Islands (Ontong Java); 1950, Sanborn and Nicholson, Fieldiana:Zool., 31:329, August 31.

Specimens examined (one male, three females, and two sex unknown; two embryos in alcohol).—Liuniuwu, Lord Howe Islands (Ontong Java) in August, USNM 278703-6, USNM 279715-6.

Measurements.—Average and extreme measurements of one male and three females are as follows: Length of head and body, 185.2 (176-196); hind foot, 34.5 (33-36); ear, 21.5 (21-23); forearm not measured [broken in all specimens examined]. Cranial measurements of a male and a female are, respectively, as follows: Greatest length of skull, 55.3, 53.8; condylobasal length,

54.2, 52.8; palatal length, 26.7, 26.0; zygomatic breadth, 30.6, 29.9; breadth of braincase, 19.9, 19.2; breadth across first upper molars, 14.3, 14.3; length of maxillary tooth-row, 20.7, 19.6; length of mandibular tooth-row, 23.1, ----.

Remarks.—Apparently *Pteropus howensis* is confined to Ontong Java (Lord Howe Islands) located northeastward of the main body of islands that constitute the Solomon Archipelago (see Fig. 5). According to A. J. Nicholson, who collected the specimens listed above, *P. howensis* is not abundant in Ontong Java. He related this circumstance to the fact that these small islands are nothing more than parts of a coral atoll used almost entirely for the production of coconuts (see Sanborn and Nicholson, 1950:329).

Specimens of *Pteropus howensis* deposited in the U. S. National Museum agree well in most ways with the original description of the species by Troughton (1931:204-205). Slight variation in color is evident; in two specimens, the mantle, just posterior to the ears, is Ochraceous-Buff.

The relationship of this species to other kinds of *Pteropus* known from Melanesia is not clear. Troughton (1931:204, 206) compared *P. howensis* with *P. hypomelanus* and *P. admiralitatum* and found that it resembled each of them. Tate (1934:2) noted that the skull of *P. admiralitatum goweri* was similar to that of *P. howensis* in structure. The latter species is, however, larger (length of forearm 122 according to Troughton, 1931:205) than any subspecies of *P. admiralitatum* (length of forearm 108-112). Also, the cheek-teeth of *P. howensis* that I have studied are relatively larger than those of either *P. hypomelanus* or *P. admiralitatum*. Furthermore, in *P. howensis* there is a small but distinct cusp located medio-posteriorly on P4 (most noticeable in young individuals) that is more reduced or undeveloped in specimens of the other two species. Cheek-teeth of *P. howensis* resemble those in a dull-colored specimen of *P. tonganus* from Fiji Island with which I compared the specimens listed above.

Weights and crown-rump lengths of the two embryos (in an advanced stage of development) examined were 20 and 29 grams and 43 and 51 mm. (apparently these are the specimens listed by Sanborn and Nicholson, 1950:329).

Pteropus tonganus

Pteropus tonganus has at least three subspecies, one of which has been recorded from the Solomons. The species ranges from a small island off the eastern coast of New Guinea, where there is an endemic subspecies, eastward to Tonga and the New Hebrides (Laurie and Hill, 1954:33-34). Felten (1964a) recently has reported on the species in the New Hebrides.

***Pteropus tonganus geddiei* MacGillivray**

1860. *Pteropus geddiei* MacGillivray, *Zoologist*, 18:7134, September, type from Aneitum Island, New Hebrides; 1912, Andersen, *Catalogue of the Chiroptera* . . . British Museum, 1:189; 1931, Sanborn, *Publ. Field Mus. Nat. Hist., Zool. Ser.*, 18:13, February 12, from Rennell Island in the Solomons.
1914. *Pteropus tonganus geddiei*, Revilliod, in Sarasin and Roux, *Nova Caledonia (A)*, 1:341; 1954, Laurie and Hill, *List of land mammals of New Guinea, Celebes and adjacent islands*, p. 34, June 30.

Specimens examined.—None.

Remarks.—*Pteropus tonganus geddiei*, as far as is known, is the widest ranging subspecies of this genus. It is the only megachiropteran in the Solomon Islands having affinities with bats to the southeast (the New Hebrides, Santa

Cruz Islands, Samoan Islands and Fiji Islands) rather than with those to the west (New Guinea). The subspecies *P. tonganus geddiei*, which ranges from the Solomons to the New Hebrides (about 500 miles straight-line distance), is said to be remarkably uniform throughout its range. Sanborn (1931:14) compared color and size in specimens from the Solomon Islands and the New Hebrides and found little variation. Another subspecies, *P. t. bascilicus* Thomas 1915, apparently closely related to *geddiei*, is known from Dampier [= Kar-kar] Island off the northeastern coast of New Guinea and therefore farther westward from the New Hebrides than are the Solomon Islands. Additional remarks on the distribution of this species are in the section on Zoogeography and Speciation.

Pteropus rayneri

Pteropus rayneri is endemic to the Solomon Islands. It is divisible into seven subspecies (see Fig. 6), which, excepting *P. r. rennelli* and *P. r. cognatus*, are strikingly colored—the mantle, back, and rump being of different colors. Differences in color and size provide characters differentiating the subspecies (see key, p. 793). Recorded lengths of forearms do not overlap between any two subspecies. *P. r. grandis*, northernmost in distribution, has the longest (about 170) forearm and *P. r. cognatus*, known from two of the southernmost islands, has the shortest (about 121).

Adult males of *Pteropus rayneri* have well-developed tufts of hair on each

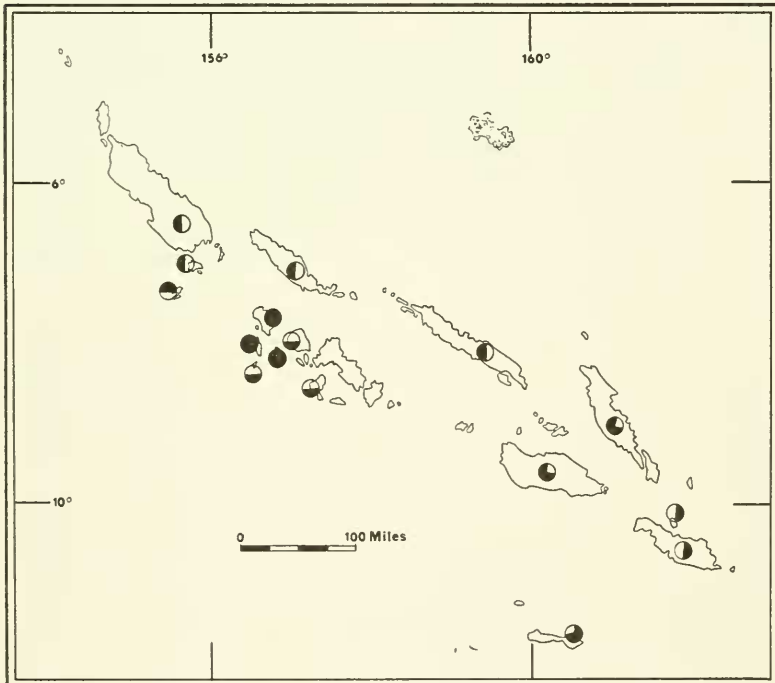


FIG. 6. Distribution of *Pteropus rayneri*: *P. r. rayneri* (●); *P. r. grandis* (◐); *P. r. lavellanus* (◑); *P. r. monoensis* (◒); *P. r. rubianus* (◓); *P. r. cognatus* (◔); *P. r. rennelli* (◕). For names of islands see Fig. 2.

side of the neck where a gland is located (see Andersen, 1912:259). Apparently these glands are not present in females as none were found in specimens studied by me or those reported by Sanborn (1931:16). Evidently, these glands are associated with sexual maturity in males because neither Sanborn nor I found them in subadult males.

Pteropus rayneri rayneri Gray

1870. *Pteropus rayneri* (part) Gray, Catalogue of monkeys, lemurs and fruit-eating bats . . . British Museum, p. 108, cotypes from Guadalcanal; 1878, Dobson, Catalogue of the Chiroptera . . . British Museum, p. 33; 1879, Trouessart, Rev. Mag. Zool., 6:204; 1879, Trouessart, Ann. Sci. Nat. Zool., 8:16; 1887, Thomas, Proc. Zool. Soc. London, p. 322, March 15; 1888, Thomas, Proc. Zool. Soc. London, p. 472, December 4; 1898, Trouessart, Catalogus Mammalium . . ., 1:78; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, p. 254; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:15, February 12, from Guadalcanal and Malaita.
1954. *Pteropus rayneri rayneri*, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 35, June 30.
1899. *Pteropus* (*Spectrum*) *rayneri* (part), Matschie, Die Megachiroptera . . . naturkunde, p. 22; 1904, Trouessart, Catalogus Mammalium . . ., Suppl., p. 51.

Specimens examined (four males and one female; one embryo in alcohol).—Guadalcanal in July and November, USNM 278700-02, USNM 278142, USNM 278714.

Measurements.—Measurements of three males and one female are, respectively, as follows: Length of head and body, —, 210, 214, 215; hind foot —, 33, 39, 42; ear, —, 23, 23, 23; length of forearm, —, 138, 136, 134; greatest length of skull, 61.5, 59.2, 61.6, 61.2; condylobasal length, 61.4, 58.2, 60.3, 60.0; zygomatic breadth, 36.6, 35.3, 35.4, 36.5; breadth of braincase, 23.7, 22.5, 22.6, 24.1; breadth across first upper molars, —, 16.9, 16.7, 16.8; width of M1, 3.4, 3.5, 3.5, 3.5; length of maxillary tooth-row, 22.4, 22.1, 23.6, 23.2; length of mandibular tooth-row, 26.4, 25.5, 25.9, 25.6.

Remarks.—*Pteropus rayneri* was named on the basis of two specimens (cotypes) obtained on Guadalcanal and listed as "male" and "female"; according to Andersen (1912:254), however, both are females.

P. r. rayneri is known from Guadalcanal and Malaita (see Fig. 6), and is of almost the same size as *P. r. cognatus*, which is known from San Cristobal and Ugi, only about 40 miles to the southeast. In the latter subspecies the back and rump are the same color (Prouts Brown), whereas in *P. r. rayneri* the rump is brightly colored and therefore contrasts strongly with the dark brown back. A specimen of *rayneri* from Malaita was reported by Sanborn (1931:15) as unusually small and having a dark-colored rump patch. In the specimens examined from Guadalcanal, there is noticeable variation in color of the mantle that does not seem related to age or sex. In two specimens (adult male and female) the mantle is Cinnamon-Rufous tinged with Russet, strongly contrasting with the crown, which is Ochraceous-Tawny and has scattered silvery hairs. Another specimen has a darker mantle (near Chestnut-Brown) and a crown of about the same color, but with a few scattered Ochraceous-Tawny hairs.

The skull of one adult male bears an extra peglike tooth posterior to M3 on the right side.

An embryo, in an advanced stage of development, in the collection of the U. S. National Museum, measures: Length of head and body, 98; hind foot, 30; ear, 8.5; length of forearm, 48 (this may be the same specimen listed by Sanborn and Nicholson, 1950:329).

Pteropus rayneri grandis Thomas

1887. *Pteropus grandis* Thomas, Ann. Mag. Nat. Hist., ser. 5, 19:147, March, type from Shortland; 1887, Thomas, Proc. Zool. Soc. London, p. 320, March 15, from Alu and Shortland; 1897, Trouessart, Catalogus Mammalium . . . , 1:80, from "I. Salomonis"; 1899, Matschie, Die Megachiroptera . . . naturkunde, p. 15; 1904, Trouessart, Catalogus Mammalium . . . , Suppl., p. 49; 1907, Miller, Bull. U. S. Nat. Mus., 57:58, June 29; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:259, from Bougainville; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:16, February 12, from Choiseul, and Santa Ysabel; 1936, Troughton, Rec. Australian Mus., 19:348, April 7; 1953, Pohle, Z. Säugetierk., 17:128, October 27.
1954. *Pteropus rayneri grandis*, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 35, June 30.

Specimens examined (six males and 10 females; five in alcohol).—Choiseul in March, 23580, 23644, 23593; Bougainville in July, August, September, and October, USNM 276926-7, USNM 276968, USNM 277091-9.

Measurements.—Average and extreme measurements of four males and seven females are as follows: Length of head and body, 281 (260-302); hind foot, 52.3 (50-58); ear, 33.1 (31-37); length of forearm, 173 (168-180). Average and extreme measurements of skulls of three males and six females are as follows: Greatest length of skull, 73.7 (71.3-77.7); condylobasal length, 73.1 (70.5-77.4); zygomatic breadth, 40 (36.4-41.5); breadth across first-upper molars, 20.9 (18.3-22.1); length of maxillary tooth-row, 28.1 (26.9-29.9); length of mandibular tooth-row, 31.8 (29.7-32.7).

Remarks.—*Pteropus rayneri grandis* is the largest subspecies of the species. It is also the widest ranging subspecies, being found on six islands (see Fig. 6).

Although the specimens listed above agree well with descriptions of color given by Thomas (1887a:147) and Andersen (1912:259, 263-264), some individual variation is noticeable. In bats not yet fully grown (judging from small size, unfused epiphyses, and lack of wear on teeth), numerous scattered hairs on the sides of the face and crown are buffy. In adults the face and crown are blackish. With regard to individual variation in color of mantle and rump patch, specimens with the following combinations were noted (1) mantle Brick Red, rump patch bright, basal three-quarters of hairs white, tips Warm Buff (2) mantle darker, near Hessian Brown, rump patch dark, Chestnut along edges, center Ochraceous-Tawny (3) mantle Brick Red, rump patch intermediate between the two other types. Size of rump patch also is variable. In some specimens it extends onto the upper parts of the thighs whereas in other specimens it does not.

Sanborn (1931:16) reported an extra tooth, behind the last lower molar, in a specimen from Choiseul. In one of three specimens in the Bishop Museum, m3 is lacking. Judging from Troughton's (1936:346) remarks, size of individuals varies considerably. Specimens that he examined from Bougainville had longer forearms (up to 177) and larger hind feet (54-57) than those examined by me from Choiseul. On the other hand, specimens listed above from Bougainville agree well with those from Choiseul. In many specimens in

the U. S. National Museum, length of the right- and left-forearm differ. For example, in No. 276926 the right forearm measures 180 whereas the left is 174; in No. 277098 the right is 172 and the left is 167. Troughton (1936:346) gave standard ear measurement in *P. r. grandis* as ranging from 29.5 to 31.5. Ears of specimens that I examined varied from 31.0 to 37.0.

Pteropus rayneri rubianus Andersen

1908. *Pteropus rubianus* Andersen, Ann. Mag. Nat. Hist., ser. 8, 2:366, October, type from Rubiana; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:255; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:15, February 12, from Narovo (Simbo).
1954. *Pteropus rayneri rubianus*, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 35, June 30.
1888. *Pteropus grandis* (part), Thomas, Proc. Zool. Soc. London, p. 470, December 4, from Rubiana; 1899, Matschie, Die Megachiroptera . . . naturkunde, p. 15; 1904, Trouessart, Catalogus Mammalium . . ., Suppl., p. 49.

Specimens examined (two males and one female).—Kolombangara, in February, 23458-60.

Measurements.—Measurements of two males and one female are, respectively, as follows: Length of head and body, 253, 265, 251; hind foot, 53, 50, 50; ear, 30, 31, 32; length of forearm, 158, 161, 160; greatest length of skull, 70.2, 67.4, —; condylobasal length, 67.0, —, 68.4; zygomatic breadth, 40.0, 39.4, 40.7; breadth across first upper molars, 19.4, 20.4, 19.9; length of mandible, 53.9, 49.4, 51.3.

Remarks.—Kolombangara Island is a new locality for *Pteropus rayneri rubianus*; heretofore this subspecies was known only from Rubiana and Narovo islands (Andersen, 1908:366; Sanborn, 1931:15). The coloration of a specimen from Narovo Island was described as between that of *P. r. rubianus* and *P. r. lavellanus*. Sanborn (1931:16) allocated it to the subspecies *rubianus* on the basis of length of forearm.

Andersen's descriptions (1908:366; 1912:256) of *rubianus* were of a specimen stored in alcohol. Coloration of the museum skins examined by me is as follows: Dorsum from shoulders to rump near Vandyke Brown; crown and mantle Brick Red; face close to Mummy Brown; rump patch and thighs close to Warm Buff, strongly contrasting with back and mantle; base of hairs dark, Seal Brown; venter dark; chest about same as back but paler laterally (to Ochraceous Tawny); throat Brick Red.

Pteropus rayneri lavellanus Andersen

1908. *Pteropus lavellanus* Andersen, Ann. Mag. Nat. Hist., ser. 8, 2:366, October, type from Vella Lavella; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:259; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:16, February 12, from Ghizo and Ronongo.
1954. *Pteropus rayneri lavellanus*, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 36, June 30.

Specimens examined (one male and one female).—Vella Lavella in November, 23192, 23142.

Measurements.—Measurements of a male and a female are, respectively, as follows: Length of head and body, 286, 282; hind foot, 55, 56; ear, 30, 30;

length of forearm, 156, 155; greatest length of skull, 72.9, 67.6; condylobasal length, 71.8, 64.2; zygomatic breadth, 38.4, 37.9; breadth across first upper molars, 19.9, 19.8; length of mandible, 54.6, 50.8.

Remarks.—*Pteropus rayneri lavellanus* inhabits islands geographically near those from which *P. r. rubianus* is known (see Fig. 6) and in most respects the two subspecies closely resemble each other. *P. r. lavellanus* is slightly the smaller (average length of forearm about 156 instead of 160) and darker. A bat from Narovo [Simbo] Island, only a few miles from Vella Lavella, identified by Sanborn (1931:16) on basis of its size as *P. r. rubianus*, resembled the subspecies *lavellanus* in color and probably represents an intergrade between the two populations.

The color of *P. r. lavellanus* is close to that of *P. r. rubianus* except that the crown, mantle, and foreneck are near Chestnut-Brown, the basal portions of hair black, and the fur of the venter, from sternum to pectoral region, is dark, almost black (compare with description of *P. r. rubianus* under account of that subspecies).

Measurements of the male examined are greater than those of the female studied. Andersen (1912:259) noted that the canine teeth are heavier in males than in females.

Pteropus rayneri monoensis Lawrence

1945. *Pteropus rayneri monoensis* Lawrence, Proc. New England Zool. Club, 23:63, March 26, type from Mono (Treasury); 1954, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 36, June 30.

Specimens examined.—None.

Remarks.—*Pteropus rayneri monoensis* is the most recently described subspecies of *P. rayneri*. Lawrence (1945:63) judged that in most ways this bat is intermediate between *P. r. grandis* and *P. r. lavellanus*. Coloration of *monoensis* indicates affinity with the former, whereas length of forearm (145-148) approaches that in the latter. The small skull, narrow palate, and whitish rump patch of *monoensis* are differences that distinguish it from *grandis* and *lavellanus*. The relatively isolated position of Mono Island may have been important in establishment of the distinctive features of this bat.

Lawrence (1945:65) quoted a collector as stating: "They [individuals of *P. r. monoensis*] rest quietly during the day in the tops of heavy-leaved, tall jungle trees, and start flying about dusk, looking for feeding spots. There is usually quite a flight for fifteen to twenty minutes at twilight. . . ."

No additional specimens of this subspecies have been collected on small adjacent islands and *monoensis* may therefore be confined to Mono Island.

Pteropus rayneri cognatus Andersen

1908. *Pteropus cognatus* Andersen, Ann. Mag. Nat. Hist., ser. 8, 2:365, October 1, type from San Cristobal; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:251; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:15, February 12, from San Cristobal and Ugi; 1954, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 35, June 30.
1962. *Pteropus rayneri cognatus*, Hill, The natural history of Rennell Island, British Solomon Islands, 4:9, February.

1870. *Pteropus rayneri* (part), Gray, Catalogue of monkeys, lemurs and fruit-eating bats . . . British Museum, p. 108, from San Cristobal; 1878, Dobson, Catalogue of the Chiroptera . . . British Museum, p. 33.
1904. *Pteropus (Spectrum) rayneri* (part), Trouessart, Catalogus Mammalium . . ., Suppl., p. 51.

Specimens examined.—None.

Remarks.—Specimens of *Pteropus rayneri cognatus* first were reported under the name *Pteropus rayneri* based on three specimens (one from San Cristobal and two from Guadalcanal). Because the description was based mostly on the two specimens from Guadalcanal, the name *rayneri* is applicable to the bats from that island. Andersen (1908:365) thought that specimens that he studied, from San Cristobal, were specifically distinct from *P. rayneri* and he proposed the name *Pteropus cognatus* for them. Later, Hill (1962:9) reduced *cognatus* to subspecific status under *P. rayneri*.

Presently *P. r. cognatus* is known only from San Cristobal and the small adjacent island of Ugi (see Fig. 6).

Pteropus rayneri rennelli Troughton

1929. *Pteropus rennelli* Troughton, Rec. Australian Mus., 17:193, September 4, type from Rennell Island; 1954, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 35, June 30.
1962. *Pteropus rayneri rennelli*, Hill, The natural history of Rennell Island, British Solomon Islands, 4:7, February.

Specimens examined.—None.

Remarks.—Until recently, *Pteropus rayneri rennelli* was known from but a single specimen. Hill (1962:7) reported two additional specimens and pointed out that *P. r. cognatus* and *P. r. rennelli* probably represent the extremes of an east-west cline in size. *P. r. rennelli* and *P. r. cognatus* differ from other subspecies of the species in lacking tricolored pelage on the dorsum, but their short rostrum clearly indicates affinity with other members of this complex group in the Solomon Islands (Hill, 1962:8).

The relationship of the subspecies *rennelli* and *cognatus* is close, both geographically and genetically. Longer forearm, longer metacarpals, and longer mandibular tooth-row serve to differentiate *rennelli* from *cognatus*.

Pteropus woodfordi Thomas

1888. *Pteropus woodfordi* Thomas, Ann. Mag. Nat. Hist., ser. 6, 1:156, February, type from Guadalcanal; 1888, Thomas, Proc. Zool. Soc. London, p. 472, December 4; 1898, Trouessart, Catalogus Mammalium . . ., 1:78; 1907, Elliot, Field Columbian Mus., Zool. Ser., 8:491; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:410, from New Georgia and Guadalcanal; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:19, February 12, from Kolombangara; 1947, Sanborn and Beecher, Jour. Mamm., 28: 389, November 19, from Banika and Guadalcanal; 1954, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 39, June 30.
1899. *Pteropus (Sericonycteris) woodfordi*, Matschie, Die Megachiroptera . . . naturkunde, p. 83; 1904, Trouessart, Catalogus Mammalium . . ., Suppl., p. 54.
1945. *Pteropus austini* Lawrence, Proc. New England Zool. Club, 23:59, March 26, from Florida.

Specimens examined (four males and three females; five in alcohol and two skin-ONLYS).—Fauro, in April, 23727, 23790; Guadalcanal in May and June, 23823, 23931; Pavuvo (Russell Islands) in August and October, USNM 277887, USNM 283872-3.

Measurements.—External measurements of two males and two females are, respectively, as follows: Length of head and body, 152, 128, 132, 155; hind foot, 29, 26, 31, 28; ear, 16, 14, 14, 17; length of forearm, 79, 76, 86, 90.

Remarks.—Heretofore, *Pteropus woodfordi* was known from New Georgia, Guadalcanal, Kolombangara, and Banika (see Fig. 7); specimens from Fauro and Pavuvo islands, listed above, provide new northern localities of record for this species.

Judging by small size and unfused epiphyses, a bat obtained in April and another obtained in June are subadults. Specimens of adults, examined by me, agree well with the descriptions of *P. woodfordi* by Thomas (1888a:156) and Andersen (1912:407-409), but are slightly smaller than specimens listed by Sanborn and Beecher (1947:389). Color of pelage in this species seems to vary. Adults seen have a pale head and mantle, contrasting strongly with the dark back. Andersen (1912:409) and Lawrence (1945:61) discussed individuals that had scattered silvery hairs mixed with dark fur dorsally and darker mantles that did not contrast noticeably with the rest of the dorsum.

Lawrence (1945:389) named *Pteropus austini* as a new species closely related to *P. woodfordi* and other species of the *P. scapulatus* group of Andersen (1912:402) and Tate (1942:336). Sanborn and Beecher (1947:389), studied a series of *P. woodfordi* from Banika and Guadalcanal and found that skulls of two subadults agreed well with cranial characteristics ascribed to *P. austini*, which was based on two subadults. Lawrence (1945:61) stated also that "the interfemoral membrane is entirely absent medially in *austini*, while in *woodfordi* it is present as a barely discernible ridge 8 mm. wide." Andersen (1912:408) had earlier reported that in the type of *woodfordi* the interfemoral membrane was "undeveloped in [the] centre." In 13 adults (in alcohol) studied by Sanborn and Beecher (1947:389), as well as in adults examined by me, the uropatagium is not present. In size, however, these specimens agree with dimensions given for *woodfordi* by Thomas (1888a:156) and Andersen (1912:410); for example, length of forearm is 93-99. According to Lawrence (1945:59) *austini*, in which the interfemoral membrane is lacking, is smaller than *woodfordi* and has a forearm of about 84. In two juveniles of *P. woodfordi* in the U. S. National Museum, the medially-developed interfemoral membrane is about 7 wide. One specimen has small but distinct calcars whereas the other (slightly larger) apparently lacks calcars. This suggests individual variation in the presence or absence, as well as in the size, of the uropatagium in *Pteropus woodfordi*.

Sanborn and Beecher (1947:389) decided that "until fully adult specimens showing the characters of *austini* are available, it best be considered a synonym of *woodfordi*." For the following reasons I agree with these authors: (1) *austini* is known from only two specimens, both of which are apparently subadults; (2) *austini* is reported to have a forearm 84 long and no interfemoral membrane, whereas *woodfordi* has a forearm about 96 long and an interfemoral membrane that is only slightly developed; (3) specimens that agree in size and cranial characters with the type of *woodfordi* but that lack an interfemoral membrane have been obtained; and (4) skulls of subadults of *woodfordi* agree with the description of skulls of *austini*.

Sanborn (1931:19) reported that specimens of *Pteropus woodfordi* were obtained at night, while feeding on young green coconuts. Lawrence (1945: 62) reported that in the late afternoon a collector found individuals of *austini* [= *woodfordi*] in the fronds of a coconut tree, apparently feeding on pollen shoots. Sanborn and Beecher (1947:388) have reported malaria (*Plasmodium*) in *P. woodfordi* obtained on Guadalcanal. They suggested that malaria might have rendered one individual helpless because when it was found, on the ground, no wounds were evident and parasites were present in the blood.

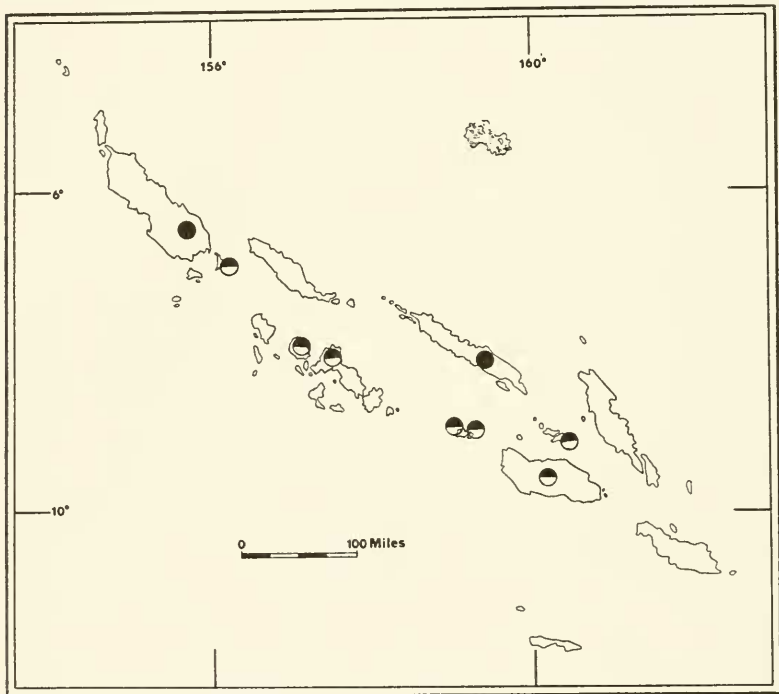


FIG. 7. Distribution of *Pteropus woodfordi* (◐) and *P. mahaganus* (●). For names of islands see Fig. 2.

Pteropus mahaganus Sanborn

1931. *Pteropus mahaganus* Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:19, February 12, type from Santa Ysabel, also reported from Bougainville; 1954, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 39, June 30.

Specimens examined (one male and two females; one in alcohol).—Bougainville, in August and October, USNM 276972, USNM 277104-5.

Measurements.—Measurements of one male and two females are, respectively, as follows: Length of head and body, 180, 204, 198; hind foot, 42, 38, 44; ear, 25, 23, 22; length of forearm, 134, 138, 140. Measurements of the skull of the male and one female are, respectively, as follows: Greatest length of skull, 52.5, 55.8; condylobasal length, 50.9, 54.3; palatal length, 24.1, 26.0;

zygomatic breadth, 28.9, 32.5; breadth across first upper molars, 14.4, 15.0; width of M1, 2.2, 2.2; length of maxillary tooth-row, 17.4, 18.4; length of mandibular tooth-row, 20.1, 21.4.

Remarks.—Sanborn (1931:19-21) described *Pteropus mahaganus* on basis of six specimens, five from Santa Ysabel and one from Bougainville. The latter was in poor condition and only provisionally allocated to this species. The specimens examined by me (listed above) confirm the occurrence of *P. mahaganus* on Bougainville.

Sanborn (1931:20) described *mahaganus* as "similar to and about the size of [*Pteropus scapulatus*] from Australia, but lighter in color," and considered it, along with *P. woodfordi*, a member of the *Pteropus scapulatus* group of Andersen (1912:402) and Tate (1942:336). I would judge, however, that *P. mahaganus* and *P. woodfordi* are much more closely related to one another than to *P. scapulatus* of Australia. The only significant characteristic that the latter has in common with the two species from the Solomons is small cheek-teeth. In fact, teeth of *scapulatus* are relatively smaller than teeth of either *mahaganus* or *woodfordi*. Also, in *scapulatus* the upper canines are widely separated due to lateral expansion of the palate at that point, whereas in *mahaganus* and *woodfordi* the width across the upper canines is relatively much less.

Dobsonia Palmer

1898. *Dobsonia* Palmer, Proc. Biol. Soc. Washington, 12:114, April 30.

1810. *Cephalotes* (part) É. Geoffroy, Ann. du Mus. d' Hist. Nat., 15:104.

Dobsonia, a genus of large to medium-sized fruit bats, occurring from Celebes to the Solomon Islands, contains at least nine species. One species and its two subspecies are endemic to the Solomons.

Dobsonia differs from all other genera of megachiropteran bats in the Solomons by combining absence of a small claw on the second digit and presence of external tail vertebrae.

The cranium of *Dobsonia* resembles, in some ways, the cranium of *Rousettus* as well as that of *Pteropus*. Even so, in *Dobsonia* the rostrum is shorter and the cheek-teeth, especially in the upper jaw, are more crowded. The anterior part of the mandible is narrow and the lower incisors are diminutive and often concealed by the flesh of the gum.

Dobsonia inermis

In a review of the genus *Dobsonia*, Andersen (1909c:532) named and described *D. inermis* and *D. nesea* from the Solomons. Specimens of *Dobsonia inermis* from San Cristobal and Ugi were said to differ from specimens of *D. nesea* from Alu, Shortland, and Rubiana in having perpendicular as opposed to anteriorly slanted upper canines. Andersen (1909c:532) reported that the two species were of ". . . the same general size." Troughton (1936:348-349) studied specimens of *Dobsonia* from Bougainville and Santa Ysabel and, because of individual variation in proclivity of the upper canines, concluded that *D. nesea* was conspecific with *D. inermis*. He (p. 349) noted that the ears were shorter in *inermis* than in *nesea*, but the size of teeth showed insular variation and a ". . . confusing amount of intergradation . . . [that obscures] . . . diagnostic importance."

Specimens of *Dobsonia* from Choiseul are smaller (externally and cranially) than those from Alu, Shortland, Rubiana, Bougainville, Fauro, Vella Lavella, Guadalcanal, Florida, Ugi, San Cristobal, and Rennell. Specimens from Santa Ysabel (see Fig. 8) are intermediate in size between those from Choiseul and the other islands listed. Judging from available specimens, two subspecies of *Dobsonia inermis* occur in the Solomons. Specimens from Choiseul (see A, Fig. 8), which are smaller than those from other islands, represent one subspecies (heretofore unrecognized), whereas specimens from other islands (except Santa Ysabel) represent a second subspecies. Specimens from Santa Ysabel are slightly larger than those on Choiseul and are regarded as intergrades between the two subspecies. Specimens from Rennell, Ugi, San Cristobal, Florida, Fauro, and Guadalcanal are slightly smaller than those from Bougainville, Vella Lavella, Shortland, and Rubiana, but the differences are not great enough to warrant recognition of two subspecies. Therefore, the subspecific name *nesea* is arranged as a synonym of *inermis*, which has priority, and the latter name is used for specimens of *Dobsonia inermis* from the Solomon islands other than Choiseul and Santa Ysabel. Additional remarks on the distribution of this species are in the section on Zoogeography and Speciation.

Pohle (1953:130) suggested that *Dobsonia inermis* (as well as *D. crenulata* and *D. praedatrix*) is conspecific with *D. viridis*, but Laurie and Hill (1954:41) did not adopt his suggestion. I have not seen adequate series of *crenulata*, *praedatrix*, and *viridis* (none of which occurs in the Solomons) to judge systematic relationships of these kinds; therefore I follow Laurie and Hill.

Dobsonia inermis inermis Andersen

1909. *Dobsonia inermis* Andersen, Ann. Mag. Nat. Hist., ser. 8, 4:532, December, type from San Cristobal; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:475.
1936. *Dobsonia inermis inermis*, Troughton, Rec. Australian Mus., 14:349, April 7, from Santa Ysabel; 1954, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 41, June 30; 1956, Hill, The natural history of Rennell Island, British Solomon Islands, 1:74, November 28, from Rennell Island.
1878. *Cephalotes peroni* (part), Dobson, Catalogue of the Chiroptera . . . British Museum, p. 91; 1879, Trouessart, Rev. Mag. Zool., 3:208; 1887, Thomas, Proc. Zool. Soc. London, p. 323, March 15, from Ugi and San Cristobal; 1888, Thomas, Proc. Zool. Soc. London, p. 476, December 4; 1897, Trouessart, Catalogus Mammalium . . ., 1:87.
1899. *Dobsonia peroni* (part), Trouessart, Catalogus Mammalium . . ., 2:1278.
1909. *Dobsonia nesea* Andersen, Ann. Mag. Nat. Hist., ser. 8, 4:532, December 1, type from Shortland Island; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:476, from Shortland, and Rubiana; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:22, February 12, from San Cristobal.
1936. *Dobsonia inermis nesea*, Troughton, Rec. Australian Mus., 14:348, April 7, from Bougainville; 1953, Pohle, Z. Säugetierk., 17:130, October 27; 1954, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 41, June 30, from New Georgia.

Specimens examined (13 males and three females; three in alcohol, crania extracted and cleaned).—Fauro in April, 23728, 23740, 23751; Vella Lavella in November, 23134-36, 23141, 23145, 23147, 23149, 23151, 23153; Guadalcanal in May and June, 23865, 23914, 24008; Florida in October, 24416.

Measurements.—See tables 2 and 3.

Remarks.—Heretofore, *Dobsonia inermis inermis* was unreported from Fauro, Vella Lavella, Guadalcanal, and Florida. Apparently the subspecies occurs on most islands of the archipelago (see Fig. 9).

In coloration and most cranial dimensions the specimens listed above agree with specimens of *D. i. inermis* from Alu, Shortland, and Rubiana (Andersen, 1909c:532; 1912:475, 476), Bougainville (Troughton, 1936:348, 349), and Rennell (Hill, 1963:74). The forearm in the adult male holotype of "*nesea*," from Shortland, is 109.5 as opposed to 109.0 in an adult female topotype of *inermis* from Ugi (Andersen, 1912:478) in the southeastern part of the archipelago (see Fig. 9). Forearms of specimens of *D. i. inermis* from Vella Lavella are 107 to 112 (measurements from labels because forearms of these specimens were broken and therefore could not be remeasured). Forearms of specimens from Fauro, Florida, Guadalcanal, and Rennell are 103.6 to 110.0 (see Hill, 1956:74). Variation in length of forearm probably is not significant because no cline is evident (see Fig. 9 and Table 2).

In 1964, 11 specimens of *Dobsonia inermis* were collected on Choiseul. They are smaller, externally and cranially, than specimens of *D. inermis* from San Cristobal, Ugi, Rennell, Guadalcanal, Florida, Rubiana, Vella Lavella, Shortland, Alu, Bougainville, and Fauro, and may be named and described as follows:

Dobsonia inermis minimus, new subspecies

Type.—Adult male, skin and skull, in good condition (originally stored in 70 per cent alcohol for about one year), no. BBM-BSIP 23716, Bernice P. Bishop Museum; from Choiseul Island, British Solomon Islands Protectorate; obtained on 20 March 1964 by Philip Temple, original number 1524.

Distribution.—Choiseul Island (type locality); intergrades from Santa Ysabel also assigned to this subspecies.

Diagnosis.—Size small for species; wing membranes, feet, and ears black; dorsal surface of interfemoral membrane sparsely set with silvery hairs, other membranes naked; hair soft, medium length (10 on mantle, 5 on crown), black hairs and scattered white hairs on face and crown; fur of dorsal surface of mantle composed of whitish hairs having faint olive cast imparting general color of Buffy-Citrine; hair of venter short (about 5), soft, and fine; general coloration Buffy-Citrine; cranium delicate; rostrum narrow in dorsal aspect (nasals not expanded laterally); forehead (junction of nasals and frontals) pronounced in lateral aspect; teeth resembling those of other subspecies of *D. inermis* but slightly smaller.

Comparisons.—From adults of *Dobsonia inermis inermis*, which occurs on Rennell, San Cristobal, Ugi, Malaita, Florida, Guadalcanal, Rubiana, Vella Lavella, Shortland, Alu, Bougainville, and Fauro, *minimus* differs in being smaller. Average length of mandible 31.2 and 33.4. For other measurements see Table 2.

From *Dobsonia praedatrix*, which occurs on New Britain, New Ireland, and Duke of York (northward of the Solomons), *minimus* differs in being smaller in all dimensions; length of forearm averaging 100.5 as opposed to 116.0, and greatest length of skull 42.4 as opposed to 50.0.

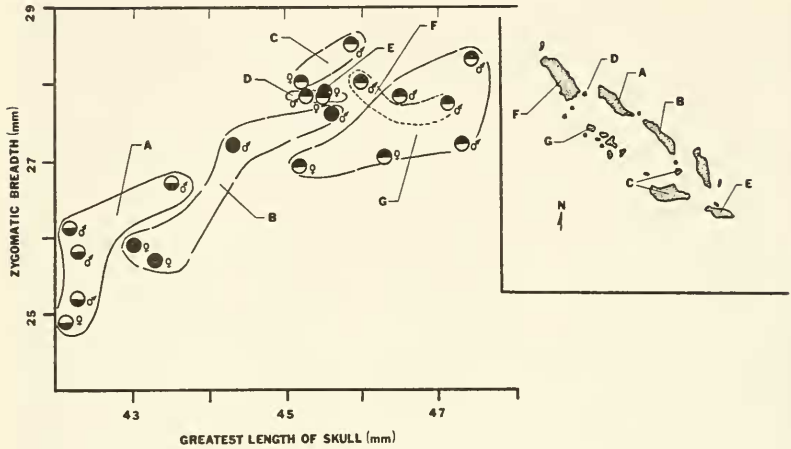


FIG. 8. Greatest length of skull plotted against zygomatic breadth for two subspecies of *Dobsonia inermis*. Symbols represent *D. i. inermis* (○), *D. i. minimus* (◐), and intergrades assigned to *minimus* (●). Capital letters are used to relate groups of specimens to the island or islands from which they were collected; spatial distribution of specimens indicated in the scatter diagram thus is shown in the inset map. Specimens from Santa Ysabel and Bougainville are deposited in the Australian Museum. The type specimen of *D. i. inermis* is labeled "E." For names of islands see Fig. 2.

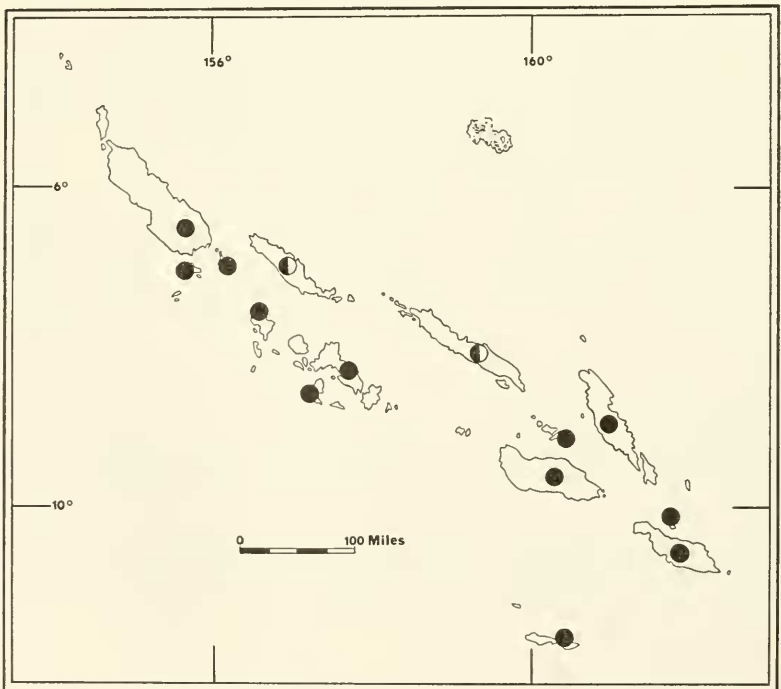


FIG. 9. Distribution of *Dobsonia inermis inermis* (●) and *D. inermis minimus* (◐). For names of islands see Fig. 2.

TABLE 2. Average and Extreme Measurements of Two Subspecies of *Dobsonia inermis*.

MEASUREMENT	<i>D. i. minimus</i>		<i>D. i. inermis</i> Guadalcanal, Fauro, Vella Lavella, Florida 9 ♂, 2 ♀
	Choiseul 4 ♂, 2 ♀	Santa Ysabel 1 ♂, 2 ♀	
	Length of head and body.....	174.5 (170 -180)	
Tail vertebrae.....	28.5 (24 - 33)	30.4 (25 - 35)
Hind foot.....	25.3 (25.1-25.9)	23.0 (21.5-24.0)	29.3 (26.0-31.6)
Ear.....	21.5 (21.0-22.9)	21.1 (21.0-21.5)	23.1 (19 - 25)
Length of forearm.....	100.5 (98.1-104.0)	105.3 (104 -107)	108.4 (105 -112)
2nd metacarpal.....	43.6 (42.6-45.2)	48.1 (45.9-50.9)
3rd metacarpal.....	61.5 (59.8-62.9)	67.6 (65.2-68.5)
4th metacarpal.....	57.5 (56.5-58.5)	62.5 (58.7-65.5)
5th metacarpal.....	59.0 (57.0-60.5)	64.4 (61.8-66.0)
Greatest length of skull.....	42.4 (42.1-43.5)	44.0 (43.0-45.6)	45.9 (45.2-47.4)
Condylbasal length.....	40.4 (39.5-41.3)	41.7 (41.1-42.6)	43.6 (43.1-45.0)
Zygomatic breadth.....	25.6 (24.9-26.8)	26.5 (25.7-27.6)	27.9 (27.2-28.5)
Breadth of braincase.....	16.8 (16.5-17.4)	18.0 (17.1-19.9)	17.9 (16.7-19.0)
Breadth across upper canines.....	8.4 (8.1- 8.7)	9.2 (9.2- 9.5)
Breadth across first upper molars.....	12.1 (11.8-12.6)	13.1 (12.6-13.3)
Length of maxillary tooth-row.....	15.6 (15.5-15.8)	16.4 (16.0-17.2)	16.4 (15.9-17.0)
Length of mandibular tooth-row.....	17.1 (16.8-17.6)	17.8 (17.3-18.4)	18.2 (17.8-19.4)

Measurements.—Comparative measurements of the subspecies *inermis* and *minimus* are given in Table 2. Some measurements of the type are as follows: Length of head and body, 147; tail vertebrae, 31; hind foot, 25; ear, 21; length of forearm, 99.5; 2nd metacarpal, 42.8; 3rd metacarpal, 62.7; 4th metacarpal, 58.5; 5th metacarpal, 59.1; greatest length of skull, 42.2; condylobasal length, 40.6; zygomatic breadth, 25.8; breadth of braincase, 16.8; length of maxillary tooth-row, 15.8; length of mandible, 31.2.

Remarks.—*Dobsonia inermis minimus* is the smallest subspecies of *Dobsonia inermis*. Specimens from Santa Ysabel, southeastward of Choiseul, are slightly larger than the type and paratypes of *minimus*. As can be seen in the scatter diagram (Fig. 8), a male from Santa Ysabel is as large as one male and most females of *D. i. inermis*. The other three specimens from Santa Ysabel also are slightly larger than specimens of *minimus* from Choiseul, but are much smaller than specimens of *D. i. inermis*, and, therefore, are referred to *D. i. minimus*.

Although there is a cline in size of *Dobsonia inermis* from Choiseul to Florida (generally southward; Fig. 9), no cline in size is apparent between Choiseul and Fauro (generally westward). Specimens of *D. inermis* from Fauro are average for the subspecies *inermis*; there is no evidence, in the small series available, of intergradation between *minimus* on Choiseul and *inermis* on Fauro.

Specimens examined (eight males and three females, all originally in alcohol; seven crania, all adults, extracted and cleaned).—Choiseul in March, 23565, 23628, 23637, 23665-67, 23640, 23714, 23716 (holotype), 23717, 23720. Ellis LeG. Troughton kindly examined and measured nos. AM-M. 3693 ♂, AM-M. 3694 ♂, AM-M. 3937 ♀, and AM-M. 3940 ♀, from Santa Ysabel in the Australian Museum.

Subfamily Macroglossinae

Macroglossus F. Cuvier

1824. *Macroglossus* F. Cuvier, Des dents des mammiferes . . . zoologiques, p. 248.
 1840. *Kidodotus* Blyth, in Cuvier's animal kingdom . . ., p. 69.
 1891. *Carponycteris* Lydekker, in Flower and Lydekker, mammals living and extinct, p. 654.
 1902. *Odontonycteris* Jentink, Notes Leyden Mus., 23:140, July 15.

Macroglossus, the widest-ranging genus of macroglossine bats, occurs from southeastern Asia to the southern islands of the Solomon Archipelago (see Ellerman and Morrison-Scott, 1966:101; Laurie and Hill, 1954:44). One species, known also from Celebes and New Guinea, occurs in the Solomons and is represented there by an endemic subspecies.

Numerous generic names have been applied, at one time or another, to bats now considered as *Macroglossus*. Trouessart (1904:65) and Miller (1907:70) listed the one bat of this genus occurring in the Solomons under *Carponycteris* and *Kidodotus*, respectively. Andersen (1911:642; 1912:767) and, later, Sanborn (1931:22) identified this bat as *Macroglossus lagochilus microtus*. Troughton (1936:350), reporting an extension of range of this species in the Solomons, used the generic name *Odontonycteris* without explanation. Andersen (1912:754) pointed out that Jentink originally established the name *Odontonycteris* on the basis of an extra premolar in each upper jaw as opposed to the usual two in *Macroglossus*, and arranged *Odontonycteris* as a synonym of *Macroglossus* because "in no genus of Megachiroptera are dental anomalies of so frequent occurrence as in *Macroglossus*, and on no point of the jaws are these

anomalies . . . so often met with as on that occupied by the molar series." Sanborn (1931:22) and Phillips (1966:27) noted variation in number of incisors in *Macroglossus* as well as in *Melonycteris*, another macroglossine genus. All of the more recent workers (Ellerman and Morrison-Scott, 1966; Pohle, 1953; Laurie and Hill, 1954) use the name *Macroglossus*.

Macroglossus lagochilus

Macroglossus lagochilus has at least three subspecies, one of which is endemic to the Solomons. The species ranges from Celebes on the west to the Solomon Islands on the east, occurring not only in New Guinea but also on many of the small adjacent islands (see Laurie and Hill, 1954:44).

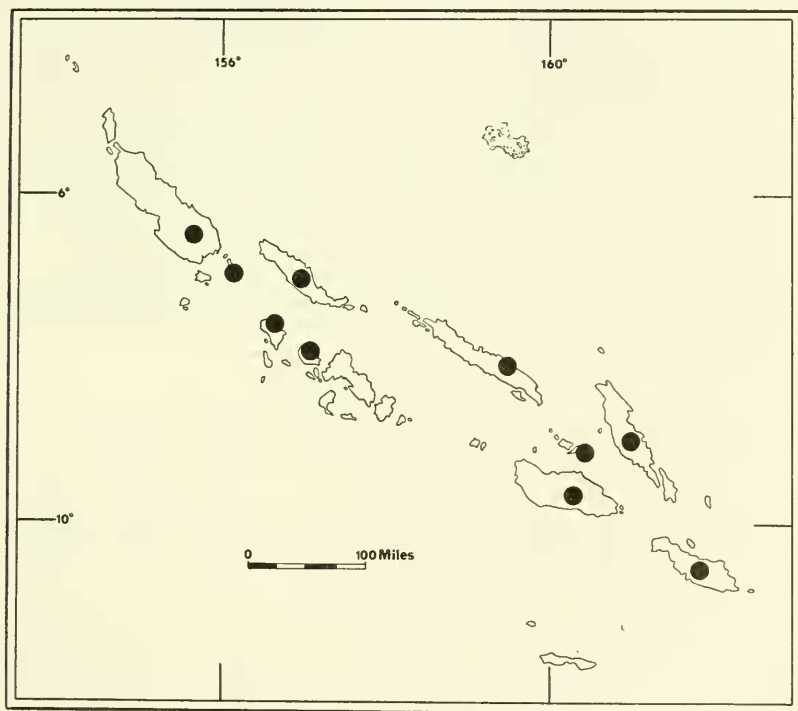


FIG. 10. Distribution of *Macroglossus lagochilus microtus*. For names of islands see Fig. 2.

Macroglossus lagochilus microtus Andersen

1911. *Macroglossus lagochilus microtus* Andersen, Ann. Mag. Nat. Hist., Ser. 8, 7:642, June, type from Guadalcanal, additional specimens from Florida; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:767; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:22, February 12, from San Cristobal; 1953, Pohle, Z. Säugetierk., 17:130, October 27, from Bougainville; 1954, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 44, June 30.
1888. *Macroglossus australis* (part), Thomas, Proc. Zool. Soc. London, p. 476, December 4, from Guadalcanal.

1904. *Carponycteris nana* (part), Trouessart, Catalogus Mammalium . . ., Suppl., p. 65.
 1907. *Kiodotus* sp., Miller, Bull. U. S. Nat. Mus., 57:70, June 29.
 1936. *Odontonycteris lagochilus microtus*, Troughton, Rec. Australian Mus., 14:350, April 7, from Bougainville.

Specimens examined (14 males and 16 females; in alcohol).—Choiseul in March, 23654-57, 23614, 23629, 23643, 23645, 23647, 23677-79, 23684; Vella Lavella in December, 23277-79, 23283-84; Fauro in April, 23765; Guadalcanal in May and June, 23830, 23864, 23935; Kolombangara in January, 23385, 23399, 23397, 23407, 23420-21; Santa Ysabel in June, 24067; Malaita in June, 24067.

Measurements.—Average and extreme external measurements of 14 males and 15 females are as follows: Length of head and body, 68.3 (63-72); tail vertebrae present but scarcely perceptible and therefore not measured; hind foot, 11.4 (9.0-12.9); ear, 12.0 (10.0-12.9); length of forearm, 37.6 (36.2-39.9).

Remarks.—The distribution of *Macroglossus lagochilus microtus* has not been well known. Specimens herein reported from Choiseul, Fauro, and Vella Lavella provide new records of distribution. As shown on Figure 10, the subspecies occurs throughout the Solomon Islands.

Macroglossus lagochilus microtus differs slightly from *M. l. nanus* Matschie, the subspecies of the Bismarck Archipelago and Admiralty Islands to the north of the Solomons. *M. l. nanus* averages slightly larger than *microtus* (see Andersen, 1912:768-769, for comparative measurements) but otherwise closely resembles it.

Individual variation is evident in several measurements of the specimens at hand (in length of forearm, for example) but no clines are apparent. Four females obtained in March were lactating, as was one taken in December and one taken in January.

Melonycteris Dobson

1877. *Melonycteris* Dobson, Proc. Zool. Soc. London, p. 119, June 1.
 1877. *Cheiropteruges* Ramsay, Proc. Linn. Soc. New South Wales, 2:19, July.
 1887. *Nesonycteris* Thomas, Ann. Mag. Nat. Hist., ser. 5, 14:147, February.

The genus *Melonycteris* is known from three species, two apparently endemic to the Solomon Islands and the third occurring in eastern New Guinea and the Bismarck Archipelago (Laurie and Hill, 1954:45).

Heretofore, the generic name *Nesonycteris* has been applied to the species in the Solomons, whereas *Melonycteris* has been restricted to the one species in the Bismarck Archipelago and New Guinea. Andersen (1912:792) judged that *Nesonycteris* was clearly distinct from *Melonycteris* on the basis of two characters (loss of a claw on the second digit and loss of the inner, lower incisors). On the other hand, he noted striking similarities in general cranial features, dentition, palatal ridges, tongue, and external appearance of the two genera. Pohle (1953:131) synonymized the two but Laurie and Hill (1954:45) considered them distinct. I have suggested previously (Phillips, 1966:26, 27) that characteristics used to distinguish between *Melonycteris* and *Nesonycteris* are of less than generic value. Variability of number of incisors in the upper jaw of specimens of *Melonycteris* (and in other macroglossine genera, as well) indicates a lack of selective pressure for either increase or decrease in number of incisors. Furthermore, the loss of the small claw on the second digit might not be important because, as Bader and Hall (1960:15) have pointed out, limbs of bats vary more in phenotypic expression than do other parts of the skeletal structure.

The discovery of a new species (*Melonycteris aurantius*) in the Solomon Islands sheds additional light on the problem. Although *M. aurantius* possesses the distinguishing characteristics of the genus "*Nesonycteris*," the species closely resembles *Melonycteris* in other features. Similarity in structure of hair of *Melonycteris* and *Nesonycteris*, as first reported by Benedict (1957:293), also supports the argument for synonymy (see Phillips, 1966:26).

Melonycteris aurantius lacks a small claw on the second digit and has only two lower incisors. In these ways this species is like *woodfordi*, which also is restricted to the Solomons. On the other hand, the structure of the skull of *M. aurantius* is like that of *M. melanops*, which is the species found in the Bismarck Archipelago.

Although *melanops* is not yet known from the Solomon Islands, I have included it in the following key.

Key to Known Species of *Melonycteris*

1. Ventral surface darker than dorsum, but not strongly contrasting with it; lacking a small claw on the second digit.....2
- 1'. Ventral surface nearly black, strongly contrasting with dorsum; small claw on second digit.....*Melonycteris melanops*
- 2(1'). Pelage bright, Cinnamon-Rufous; postorbital region of skull expanded (about 8.3 wide).....*Melonycteris aurantius*, p. 816
- 2'. Pelage dark, near Wood-Brown or Cinnamon; postorbital region of skull constricted (about 7.5).....*Melonycteris woodfordi*, p. 816

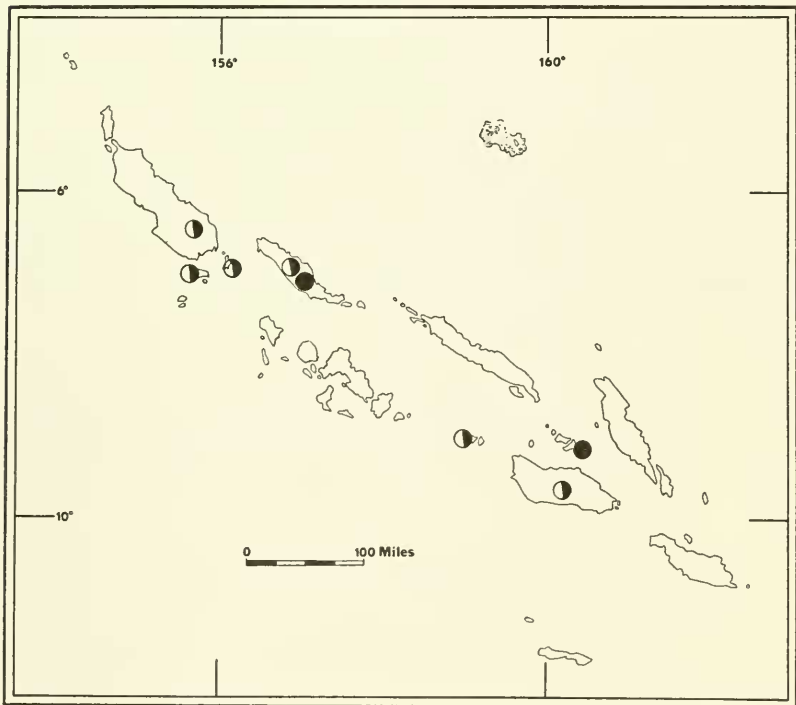


FIG. 11. Distribution of *Melonycteris aurantius* (●) and *M. woodfordi* (◐). For names of islands see Fig. 2.

Melonycteris aurantius Phillips

1966. *Melonycteris aurantius* Phillips, Jour. Mamm., 47:23-27, March 12, type from Florida Island, additional specimens from Choiseul Island.

Specimens examined (six females; three in alcohol).—Florida in October, 24440; Choiseul in March, 23615, 23617, 23558, 23694, 23681.

Measurements.—Average and extreme measurements of six females are as follows: Length of head and body, 80.8 (77-106); hind foot, 17.2 (16.0-18.7); ear, 12.7 (11.5-14.0); length of forearm, 49.3 (42.9-53.8). Average and extreme measurements of skulls of five females are as follows: Greatest length of skull, 31.8 (30.8-33.3); condylobasal length, 29.7 (28.6-32.4); zygomatic breadth, 18 (17.2-20.0); breadth of braincase, 12.6 (12.4-13.2); postorbital breadth, 8.3 (8.0-8.9); length of maxillary tooth-row, 10.1 (9.4-10.4); length of mandibular tooth-row, 11.7 (10.8-12.2).

Remarks.—On Choiseul Island *Melonycteris aurantius* was taken at the same locality as its congener, *Melonycteris woodfordi*.

Externally, *M. aurantius* resembles *M. woodfordi*. These species are the same size, but the former is brighter in color (nearly orange in adults) than the latter, which is Wood-Brown dorsally. Internally, differences between *M. aurantius* and *M. woodfordi* are more obvious. In the skull of *M. aurantius*, the postorbital region is expanded (measuring about 8.3), whereas in *M. woodfordi* the postorbital region is constricted. Furthermore, in lateral aspect the posterior portion of the skull of *M. aurantius* is down-turned and the angle of the facial axis with the basicranial axis is much more acute than in *M. woodfordi*.

The number of upper incisors is highly variable in the six specimens of *M. aurantius* that I have examined. In two specimens an extra tooth has erupted just anterior to I2 and there is a total of six upper incisors. In two other specimens an extra tooth has erupted in front of I2 on one side but not the other. I could find no trace of an extra tooth in the remaining two specimens.

Practically nothing is known about the natural history of *M. aurantius*, or, indeed, that of either of the other two species of this genus. One field collector (Temple, *in litt.*) for the Bishop Museum reported that he obtained both *M. aurantius* and *M. woodfordi* in the same mist net in one night. The holotype, an adult female, was lactating when obtained in October.

Melonycteris woodfordi (Thomas)

1887. *Nesonycteris woodfordi* Thomas, Ann. Mag. Nat. Hist., ser. 5, 14:147, February, type from Shortland Island; 1887, Thomas, Proc. Zool. Soc. London, p. 324, March 15; 1888, Thomas, Proc. Zool. Soc. London, p. 476, December 4; 1898, Trouessart, Catalogus Mammalium . . . , 1:90; 1899, Matschie, Die Megachiroptera . . . naturkunde, p. 91; 1904, Trouessart, Catalogus Mammalium . . . , Suppl., p. 66; 1907, Miller, Bull. U. S. Nat. Mus., 57:74, June 29; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:792, from Alu, Shortland, Fauro, and Guadalcanal; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:23, February 12, from Russell Island (Pavuvu); 1954, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 45, June 30.
1953. *Melonycteris woodfordi*, Pohle, Z. Säugetierk., 17:130, October 27, from Bougainville Island; 1966, Phillips, Jour. Mamm., 47:23, March 12, from Choiseul.

Specimens examined (three males and one female; in alcohol).—Choiseul, in April, 23413-14, 23434, 23275.

Measurements.—Average and extreme measurements of three males and one female are as follows: Length of head and body, 86.1 (83.1-91.0); hind foot, 19.6 (17.2-22.2); ear, 11.3 (10.8-11.7); length of forearm, 54.4 (52.1-57.7).

Remarks.—Specimens of *Melonycteris woodfordi* from Choiseul constitute a new locality of occurrence for the species. Apparently *M. woodfordi* occurs throughout the Solomons (see Fig. 11).

Thomas (1887a:147) named *Nesonycteris woodfordi* in a preliminary report that appeared before the publication of the more detailed description of the genus and species (1887b:323-324). In the second paper he stated that the anterior projections of the premaxillary bones are separated distinctly in both *Nesonycteris* and *Melonycteris*. According to Thomas (1887b:323), it was by some "accident" that Dobson (1878:4) reported the anterior projections of the premaxillary bones in *Melonycteris melanops* to be united. Writing at a later date, Andersen (1912:785) reported that in *Melonycteris melanops* the premaxillary bones have "simple contact with each other." Furthermore, in Andersen's (1912:791) illustration of *M. woodfordi* the premaxillary bones are in contact anteriorly. In specimens of *woodfordi* and *melanops* examined by me, the premaxillary bones are in contact. In *M. aurantius* the premaxillary bones are not in contact, and it differs from *woodfordi* in several other respects.

In *M. woodfordi*, as in other macroglossine bats, there is variability in dentition. One specimen examined has a total of three upper incisors, and another had an extra peglike tooth just anterior to I 1.

Subfamily Nyctimeninae

Nyctimene Borkhausen

1797. *Nyctimene* Borkhausen, Deutsche fauna . . ., 1:86.
 1810. *Cephalotes* É. Geoffroy, Ann. du Mus. d' Hist. Nat., 15:104.
 1811. *Harpyia* Illiger, Prodr. Syst. Mamm. et Avium, p. 118.
 1837. *Gelasinus* Temminck, Monographie de Mammalia . . ., 2:100.

Tube-nosed bats of the genus *Nyctimene* occur from Celebes on the west to the Santa Cruz Islands on the east. Heretofore, two species (*N. albiventer* and *N. major*), each with an endemic subspecies, were known from the Solomon Islands. Both species occur also in New Guinea and on many adjacent islands. A new species of *Nyctimene*, apparently endemic to the Solomons, and a new subspecies of *N. albiventer* are named beyond.

Nyctimene is related closely to *Cynopterus* and the "Cynopterus group" of Andersen (1912:691). Because *Nyctimene* is a highly specialized bat, Miller (1907:75) placed it in a subfamily separate from that of *Cynopterus* and its allies.

Andersen (1912:696, 697) placed the species of *Nyctimene* previously known from the Solomons in two groups, the "papuanus" group and the "cephalotes" group, on the basis of difference in length of forearm and length of maxillary tooth-row. Because of its short forearm (about 58), *N. albiventer* is in the *papuanus* group; and *N. major*, because of its long forearm (about 74), is in the *cephalotes* group.

male from Kolombangara is unusually dark, almost black; color of the other specimens (all in alcohol) is consistent according to sex.

Nyctimene albiventer from Choiseul and Santa Ysabel is smaller, in all respects, than *N. albiventer* from Bougainville, Kolombangara, and Guadalcanal (see Table 3), and therefore may be named and described as follows:

Nyctimene albiventer minor, new subspecies

Type.—Adult male, skin and skull, in good condition (originally stored in alcohol for about one year), no. BSIP 23636, Bernice P. Bishop Museum; from Choiseul Island, British Solomon Islands Protectorate; obtained on 11 March 1964, by Philip Temple, original number 1441.

Distribution.—Known only from Choiseul and Santa Ysabel islands (see Fig. 12).

Diagnosis.—Small for *Nyctimene*; wing membranes brown with scattered yellow spots (dried specimens); uropatagium, feet, and ears brown; dorsum of tibia set with hair, ventral surface naked; dorsum of uropatagium sparsely set with pale brown hairs, ventral surface almost bare; fringe of hairs along two centimeters of dorsal and ventral surfaces of trailing edge of wing membrane; proximal third of dorsal surface of forearm sparsely set with hairs; pelage of back soft and thick, of medium length (about 7); hair on crown and nape short (about 4); well-defined black dorsal stripe, extending from uropatagium to shoulders; skull resembling that of other subspecies of *N. albiventer* but relatively smaller; zygomatic arch delicate, slender anteriorly; P2 small (see Fig. 14). Sexually dichromatic as follows: male—dorsum Hair-Brown, bases of hairs darker; hair on throat sparse, medium length (about 6), Hair-Brown; fur along sides of abdomen Drab; female—dorsum having Buffy-Brown cast, some individual hairs Hair-Brown; shoulders Sayal-Brown; hair on throat sparse, Hair-Brown on throat and mid-line of abdomen; sides of abdomen Sayal-Brown.

Comparisons.—From *Nyctimene major scitulus*, the largest member of this genus in the Solomons, *N. a. minor* differs in being smaller in all measurements taken; forearm averaging 54.8 as opposed to 73.5; greatest length of skull 28.2 as opposed to 37.0, and females pale brown instead of pale gray.

From nine adults of *Nyctimene albiventer bougainville* from Bougainville, Kolombangara, and Guadalcanal, *minor* differs as follows: averaging slightly smaller in all dimensions; forearm averaging 54.8 as opposed to 57.9; second metacarpal averaging 27.4 as opposed to 28.3; 5th metacarpal averaging 38.5 as opposed to 40.0; condylobasal length 26.7 as opposed to 28.0; length of mandibular tooth-row 10.3 as opposed to 10.9; mandible smaller (see Fig. 14); dorsal stripe fainter.

From *Nyctimene albiventer papuanus*, known from eastern New Guinea, New Britain, and the Admiralty Islands, *minor* differs as follows: slightly smaller in most dimensions; forearm averaging 54.8 as opposed to 57.0; length of maxillary tooth-row 8.9 as opposed to 9.8; length of mandibular tooth-row 10.3 as opposed to 11.0; breadth across upper third premolars notably less (7.5 as opposed to 8.4).

N. a. minor differs from *N. albiventer albiventer* Gray, which occurs about 800 miles to the west of *minor*, in ways made apparent by the description by Andersen (1912:700-701). *N. a. minor* occurs about 1500 miles eastward of the place from which *N. a. draconilla* Thomas, a subspecies essentially unknown to me, was named (see Laurie and Hill, 1954:46).

From *Nyctimene sanctacrucis*, known from the Santa Cruz Islands, *minor* differs as follows: much smaller in all dimensions; forearm averaging 54.8 as opposed to 75; greatest length of skull 28.2 as opposed to 34.5; length of maxillary tooth-row 8.9 as opposed to 12.9.

Measurements.—Measurements of the two subspecies from the Solomons are given in Table 3. Some measurements of the type are as follows: Length of head and body, 108; tail vertebrae, 20.5; hind foot, 14.7; ear, 11.3; length of

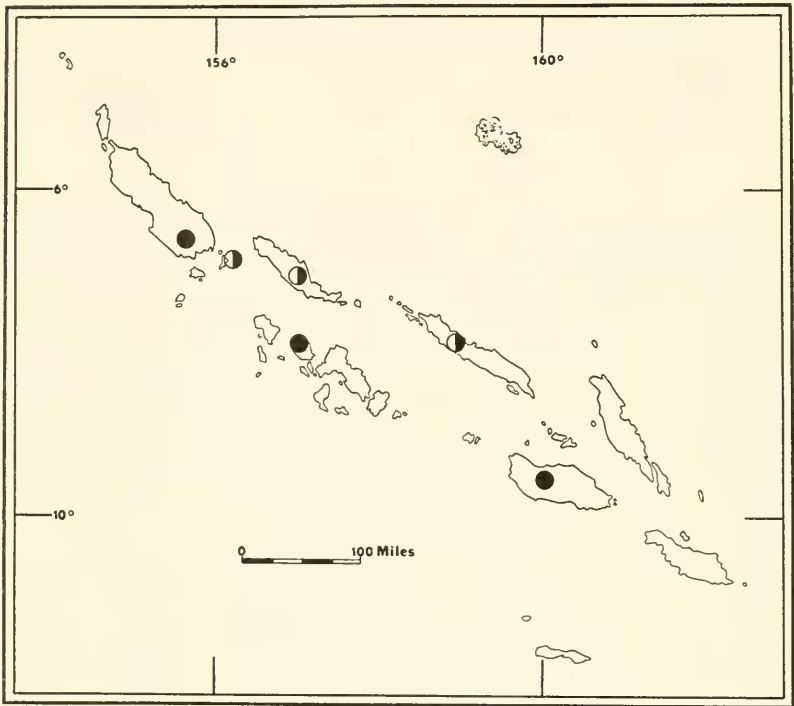


FIG. 12. Distribution of *Nyctimene albiventer bougainville* (●) and *N. albiventer minor* (◐). For names of islands see Fig. 2.

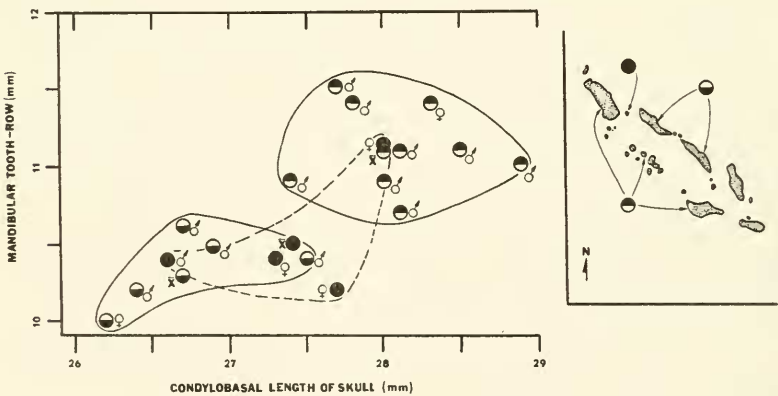


FIG. 13. Scatter diagram comparing two subspecies of *Nyctimene albiventer*. One individual of specimens thought to be intergrades is as large as specimens of *Nyctimene a. bougainville*, whereas the other three intergrades are about the same size as specimens of *N. a. minor*. Symbols represent *N. a. bougainville* (●), *N. a. minor* (◐), and intergrades assigned to *minor* (●). For names of islands see Fig. 2.

TABLE 3. Average and Extreme Measurements of *Nyctimene albiventer bougainville* and *N. a. minor*.

MEASUREMENT	<i>N. a. minor</i>	Intergrades	<i>N. a. bougainville</i>
	Choiseul, Santa Ysabel 4 ♂, 1 ♀	Fauro 1 ♂, 3 ♀	Kolombangara, Guadalcaanal 8 ♂, 1 ♀
Length of head and body.....	107.0 (105 -109)	109.2 (105 -112)	110.0 (106 -117)
Tail vertebrae.....	20.0 (19.3-20.5)	21.0 (20 -22)	19.2 (15.5-23.0)
Hind foot.....	14.2 (13.5-15.0)	14.3 (13.0-15.9)
Ear.....	11.9 (11.0-13.0)	12.8 (11.8-14.5)
Length of forearm.....	54.8 (54.0-55.8)	57.1 (55.9-59.0)	57.9 (55.8-59.8)
Greatest length of skull.....	28.2 (27.2-28.9)	28.6 (28.3-29.7)	29.7 (28.6-30.1)
Condylobasal length.....	26.7 (26.2-27.5)	27.4 (26.6-28.0)	28.0 (27.8-28.9)
Palatal length.....	11.2 (10.9-11.9)	11.6 (11.3-11.8)	11.7 (11.0-12.5)
Breadth of braincase.....	12.0 (11.5-12.4)	12.0 (11.7-12.2)	12.3 (12.1-12.8)
Zygomatiac breadth.....	18.9 (18.4-19.7)	18.6 (18.4-19.2)	19.2 (18.7-20.0)
Interorbital breadth.....	5.0 (4.7-5.6)	5.3 (5.0-5.6)	5.1 (4.7-5.5)
Breadth across first upper molars.....	8.6 (8.4-8.9)	8.9 (8.7-9.1)	9.1 (8.8-9.6)
Maxillary tooth-row.....	8.9 (8.7-9.3)	9.3 (9.1-9.5)	9.5 (9.2-9.8)
Mandibular tooth-row.....	10.3 (10.0-10.6)	10.5 (10.2-11.1)	10.9 (10.7-11.4)

forearm, 55.1; 2nd metacarpal, 27.4; 3rd metacarpal, 39.0; 4th metacarpal, 37.5; 5th metacarpal, 39.1; greatest length of skull, 28.6; condylobasal length, 27.5; zygomatic breadth, 18.4; length of maxillary tooth-row, 9.0; length of mandibular tooth-row, 10.4.

Remarks.—*Nyctimene albiventer minor* closely resembles *N. albiventer bougainville*, differing from the latter mostly in size. Although adults of *minor* average only slightly smaller than adults of *bougainville* (see Table 3), there is only slight overlap (about 0.2 at most) in most minimum dimensions of external and cranial features of *bougainville* and corresponding maximum dimensions of externals and crania of *minor*. The difference in size is clearly shown in Figs. 13 and 14.

Four specimens of *Nyctimene albiventer* from Fauro herein are considered to be intergrades between *N. a. bougainville* and *N. a. minor*. As shown in Table 3, the specimens from Fauro average slightly larger than those of *minor* from Choiseul and Santa Ysabel and slightly smaller than specimens of *bougainville* from Kolombangara and Guadalcanal. I have assigned the specimens from Fauro to *N. a. minor* because they generally are closer to *minor* in size (see Fig. 13).

Specimens examined (five males and four females; seven in alcohol; seven crania extracted and cleaned).—Choiseul in February and March, 23636 (holotype), 23631, 23540, 23646; Santa Ysabel in February, 23539; Fauro in April, 23742, 23743, 23763, 23764.

One specimen of *Nyctimene* from Malaita Island is smaller than *Nyctimene major*, which is known from Shortland, Alu, Florida, New Georgia, Guadalcanal, Choiseul, and Malapa (see Fig. 15) and is larger than either of the two subspecies of *Nyctimene albiventer* known from Bougainville, Fauro, Kolombangara, Guadalcanal, Choiseul, and Santa Ysabel. This specimen represents a previously unknown species and may be named and described as follows:

Nyctimene malaitensis, new species

Type.—Adult female, skin and skull, in good condition (originally stored in alcohol for about one year), no. BSIP 24103, Bernice P. Bishop Museum; from Malaita Island, British Solomon Islands Protectorate; obtained on 1 July 1964, by Peter Shanahan, original no. unknown.

Distribution.—Known only from Malaita (see Fig. 16).

Diagnosis.—Size average for genus but larger than closest relative, *Nyctimene albiventer*; wing membranes brown with scattered yellow spots (dried specimen); uropatagium, ears, and feet brown; dorsal surface of tibia set with hair, ventral surface bare; dorsal surface of uropatagium sparsely set with hair, ventral surface having few, scattered hairs; dorsal surface of trailing edge of wing membrane sparsely set with hairs, ventral surface bare; proximal third of upper- and under-surface of forearm set with hair; pelage of back luxuriant and soft (about 10 long); hair on crown and nape shorter than on back (4 to 8); well-defined black dorsal stripe from shoulders to rump (about 2 wide); basal half of most hairs on dorsum Deep Mouse Gray, distal half Light Buff, tips Ochraceous-Tawny; some hairs on back entirely Light Buff; hairs of crown Light Ochraceous Buff tipped with Ochraceous-Tawny; hair on throat and along sides of abdomen Light Ochraceous Buff; hairs of ventral midline Smoke Gray; braincase narrow; zygomatic breadth relatively narrow; well-developed lambdoidal crest in female; rostrum short, wide; upper canines slanted posteriorly; upper incisors large; foramen ovale large (see Fig 14).

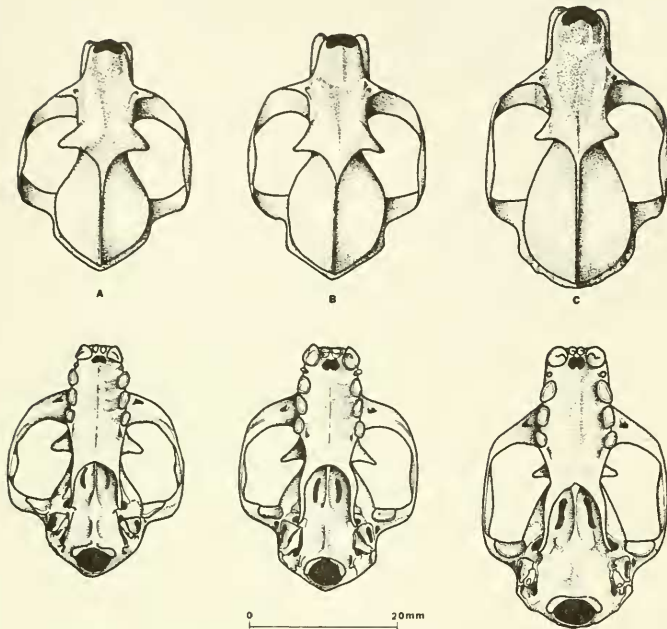


FIG. 14. Dorsal and ventral views of skulls of (A) *Nyctimene albiventer minor* [specimen 23631 ♂], (B) *N. a. bougainville* [specimen 23381 ♂], and (C) *N. malaitensis* [specimen 24103 ♀].

Comparisons.—From *Nyctimene major scitulus*, the largest kind of *Nyctimene* in the Solomons, *malaitensis* differs as follows: smaller in all dimensions (forearm 65 as opposed to 73.5); greatest length of skull 32.4 as opposed to 37.0; length of maxillary tooth-row 10.5 as opposed to 13.0; length of mandibular tooth-row 11.8 as opposed to 14.2.

From nine adults of *Nyctimene albiventer bougainville* from Bougainville, Kolombangara, and Guadalcanal, *malaitensis* differs as follows: larger in all dimensions: forearm 65 as opposed to 57.9; greatest length of skull 32.4 as opposed to 29.7; zygomatic breadth 20.4 as opposed to 19.2; and length of maxillary tooth-row 10.5 as opposed to 9.5; length of mandibular tooth-row 11.8 as opposed to 11.1.

From five adults of *Nyctimene albiventer minor*, from Choiseul and Santa Ysabel, *malaitensis* differs in the same ways it differs from *N. a. bougainville*, but the contrast is even greater when *malaitensis* and *minor* are compared.

From *Nyctimene santacrucis*, known only from the Santa Cruz Islands, *malaitensis* differs in being smaller in all dimensions: forearm 65 as opposed to 75; greatest length of skull 32.4 as opposed to 34.5; and length of maxillary tooth-row 10.5 as opposed to 12.9.

Measurements of the holotype.—Length of head and body, 118; tail vertebrae, 23.0; hind foot, 16.0; ear, 14.0; length of forearm, 65.0; 2nd metacarpal, 33.2; 3rd metacarpal, 46.4; 4th metacarpal, 44.3; 5th metacarpal, 46.0; greatest length of skull, 32.4; condylobasal length, 30.6; palatal length, 13.0; breadth of braincase, 12.5; zygomatic breadth, 20.4; interorbital breadth, 5.5; breadth across first upper molars, 9.5; length of maxillary tooth-row, 10.5; length of mandibular tooth-row, 11.8.

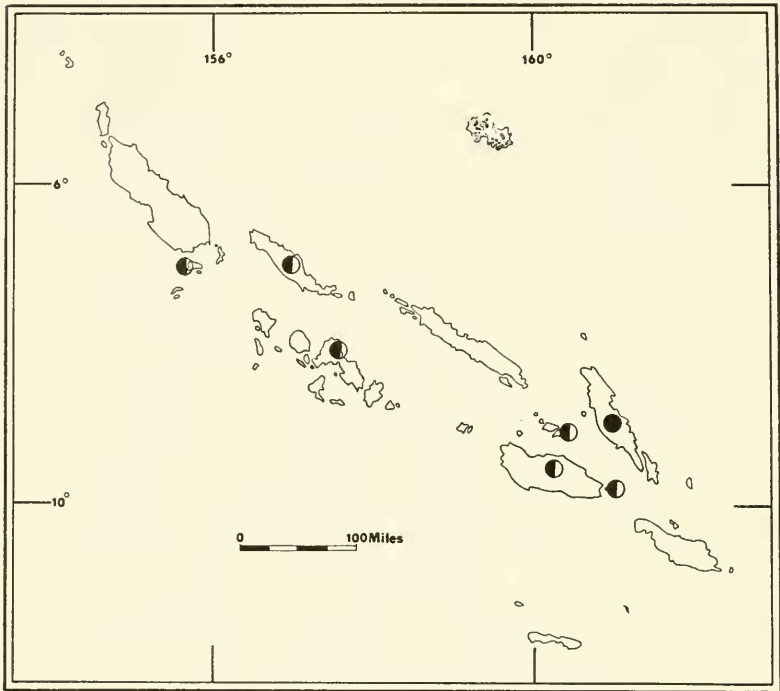


FIG. 15. Distribution of *Nyctimene malaitensis* (●) and *N. major scitulus* (◐). For names of islands see Fig. 2.

Remarks.—In size, *Nyctimene malaitensis* is intermediate between *N. albiventer* and *N. major*. Because the type of *malaitensis* is brown and not pale gray, as are females of *major*, *N. malaitensis* most likely is more closely related to *N. albiventer*, in which the females are brown. The teeth of the holotype and only known specimen of *malaitensis* are too worn to be useful in determining the relationships between these species.

When more specimens are available, *N. malaitensis* may prove to be a subspecies of *N. albiventer*. At present, *malaitensis* is accorded specific rank in order not to obscure the apparent relationships of *N. albiventer bougainville* and *N. a. minor*. Additionally, *N. malaitensis* is given specific rank because (1) it is larger (especially in external dimensions) than the largest subspecies of *N. albiventer* (compare above measurements with those in Table 3), and (2) *malaitensis* does not form a cline with either of the two subspecies of *N. albiventer*.

Specimen examined (one female).—Malaita in July, 24103 (holotype).

Nyctimene major

This large species of tube-nosed bat has at least four subspecies, one of which (*N. major scitulus*) is endemic to the Solomons. The species occurs throughout eastern New Guinea and on many of the islands adjacent to the

eastern coast of New Guinea, including the Trobriand Islands, the Bismarck Archipelago, and the Solomons (see Laurie and Hill, 1954:47). The geographic distribution of the species generally is the same as that of *N. albiventer*.

In *Nyctimene major*, as in *N. albiventer*, most males are grayish-brown, whereas most females are pale gray.

Nyctimene major scitulus Andersen

1910. *Nyctimene scitulus* Andersen, Ann. Mag. Nat. Hist., ser. 8, 6:623, December 1, type from Shortland; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:711, from Shortland, New Georgia, Florida, Guadalcanal; 1931, Troughton, Proc. Linnean Soc. New South Wales, 56:206, July 15; 1931, Sanborn, Publ. Field Mus. Nat. Hist., 18:22, February 12, from Choiseul and Malapa; 1942, Tate, Bull. Amer. Mus. Nat. Hist., 80:342, December 31.
1954. *Nyctimene major scitulus*, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 47, June 30.
1862. *Harpyia pallasi*, Gerrard, Catalogue of the bones . . . British Museum, p. 58.
1870. *Harpyia cephalotes*, Gray, Catalogue of monkeys, lemurs and fruit-eating bats in the British Museum, p. 121.
1878. *Harpyia major*, Dobson, Catalogue of the Chiroptera . . . British Museum, p. 90; 1879, Trouessart, Rev. Mag. Zool., 3:207; 1887, Thomas, Proc. Zool. Soc. London, p. 323; 1888, Thomas, Proc. Zool. Soc. London, p. 476; 1897, Trouessart, Catalogus Mammalium . . ., 1:87.
1899. *Cephalotes major*, Trouessart, Catalogus Mammalium . . ., 2:1277.
1899. *Gelasinus major*, Matschie, Die Megachiroptera . . . naturkunde, p. 84; 1904, Trouessart, Catalogus Mammalium . . ., Suppl., p. 64.

Specimens examined (four males and one female; dried skins with skulls inside).—Florida in October, 24397, 24413, 24418, 24419.

Measurements.—External measurements of four males and one female are, respectively, as follows: Length of head and body, 134, 128, 134, 134, 136; tail vertebrae, 28, 23, 27, 26, 21; hind foot, 20, 16, 19, 16, 21; ear, 17, 17, 17, 17, 18; length of forearm, 73.8, 68.0, 74.0, 73.6, 78.0.

Remarks.—*Nyctimene major scitulus* has been recorded only from the western chain of islands in the Solomons (see Fig. 15). Specimens examined by me agree well in external dimensions and color with specimens described by Andersen (1912:712) and Troughton (1931:206-207).

ZOOGEOGRAPHY AND SPECIATION

De Beaufort (1951:113) considered bats of "less zoogeographical importance" than other mammals because the ocean is not an "absolute barrier to their dispersal." Volant animals are ecologically terrestrial and therefore are more nearly earthbound than De Beaufort's remarks would suggest (see Miller, 1966:10). Indeed, many kinds of volant animals are endemic to the Solomons. Birds, for example, are well adapted for flight but pose some of the most complex zoogeographic problems in the area of New Guinea and the Solomon Islands (Mayr, 1940:198; 1942:81-83; Koopman,

1957). Rapid speciation can take place in any situation where there is a high degree of isolation (Wright, 1931; Lack, 1947). In fact, isolation is a most important factor in speciation of insular populations (Baker, 1951:55). The one genus, nine species, and 19 subspecies of megachiropterans that are endemic to the Solomons (Table 4) obviously indicate that bats, although volant, can be restricted to one or more islands long enough for new taxa to evolve.

The megachiropteran bats of the Solomons have their affinities with the fauna of New Guinea (Table 4); the Solomons and New

TABLE 4. A Summary of the Kinds of Megachiropteran Bats in the Solomon Islands and Their Affinities with Faunas of Adjacent Islands.

	Totals	Endemic to Solomons	Common only to Solomons and Bismarcks	Common to Solomons, Bismarcks, and New Guinea	Common to Solomons, New Hebrides, and New Caledonia
Genera....	7	1	0	6	0
Species....	16	9	1	6	1
Subspecies	20	19	0	0	1

Guinea have six genera and six species in common. Because the two areas never have been connected (*via* the Bismarck Archipelago) by dry land, bats probably have reached the Solomons by flying from island to island (see Durham, 1963:357, 359, 361, 363). Deignan (1963:266) has dismissed voluntary or involuntary flight as possible explanations for distributions of bats and birds on islands of the Pacific.

The taxonomic level of endemism can be used as an indicator of antiquity (Dobzhansky, 1941; Koopman, 1958:429-430). The one megachiropteran genus (*Pteralopex*) endemic to the Solomons apparently is an ancient relic. Bats of this monotypic genus occur on Bougainville, Choiseul, Santa Ysabel, and Guadalcanal (see Fig. 4). These four islands probably were contiguous during the maximum lowering of sea level in the Pleistocene (see Durham, 1963:362-363). Bats of the genus *Pteralopex* are the only kind in the Solomons having a distribution that can be correlated with former land connections between islands.

The distributions of 16 species of megachiropterans known from the Solomons are summarized in Table 5 and in Figure 16. The larger islands (in terms of surface area and elevation) in general

have the highest number of species (Guadalcanal 10, Choiseul 9, and Bougainville 8). But Fauro, one of the smallest islands for which data are available, has six species of megachiropterans whereas San Cristobal and Malaita, two of the larger islands, have only three and four species, respectively. Possibly this difference signals the need for additional collecting.

Bougainville and Choiseul, about 60 miles apart, have seven species of megachiropterans in common (Table 5). Fauro, 25 miles southeast of Bougainville and 35 miles west of Choiseul, shares five species with each of these islands (Fig. 16). *Pteralopex atrata* and *Pteropus rayneri* occur on Choiseul and on Bougainville, but not on Fauro. Individuals of these species are the largest fruit bats in the Solomons, and their absence on Fauro suggests, therefore, that this small island is ecologically unsuitable, at least in some months, for the support of populations of bats that require relatively large amounts of food. The small size of the island is consistent with this hypothesis, but several other islands as small as Fauro do support populations of the large kinds of *Pteropus*, at least in some months.

Santa Ysabel has six species of megachiropterans and 10 occur on Guadalcanal (Table 5). These two islands, separated by about 100

TABLE 5. A Summary of Distribution of All Species of Megachiropteran Bats Known from the Solomons. Only Islands Well Known Faunistically Are Listed.

SPECIES	Bougainville	Choiseul	Santa Ysabel	Ndai	Malaita	Florida	Fauro	Shortland	Vella Lavella	Kolombangara	Russell	Guadalcanal	San Cristobal	Ugi	Rennell	Ontong Java
<i>R. amplexicaudatus</i>	X	X	X		X		X			X		X				
<i>P. atrata</i>	X	X	X									X				
<i>Pt. hypomelanus</i>				X				X	X		X	X				
<i>Pt. admiralitatum</i>											X	X				
<i>Pt. tonganus</i>											X	X				
<i>Pt. howensis</i>															X	
<i>Pt. rayneri</i>	X	X	X		X				X		X	X	X	X	X	
<i>Pt. woodfordi</i>							X		X	X	X	X				X
<i>Pt. mahaganus</i>	X	X	X													
<i>D. inermis</i>	X	X	X		X	X	X	X	X			X	X	X	X	
<i>M. lagochilus</i>	X	X	X			X	X	X		X		X	X			
<i>M. woodfordi</i>	X	X	X				X	X			X	X	X			
<i>M. aurantius</i>						X	X			X		X				
<i>N. albiventer</i>	X	X	X			X		X				X				
<i>N. major</i>					X	X						X				
<i>N. malaitensis</i>																
Totals	8	9	6	1	4	4	6	4	3	5	4	10	3	2	3	1

these small islands can support only limited numbers of individuals during part of a year.

Some of the small islands in the Solomons have populations of large fruit bats. For example, *Pteropus admiralitatum* and *P. hypomelanus* have been reported from the small islands in the Russell Group (Table 5). Possibly these species do not live concurrently in the Russells; specimens of the two were obtained in different years. Two small megachiropterans, *P. woodfordi* and *Melonycteris woodfordi*, also inhabit the Russells. Shortland, a small island about 15 miles south of Bougainville, supports one large bat, *P. admiralitatum*, as well as smaller megachiropterans.

Kolombangara and Vella Lavella are about the same size and are separated by about 15 miles of water. *Rousettus amplexicaudatus*, *Pteropus rayneri*, *P. woodfordi*, *Macroglossus lagochilus*, and *Nyctimene albiventer* have been collected on Kolombangara but only *P. admiralitatum*, *P. rayneri*, and *Dobsonia inermis* have been found on Vella Lavella. The difference in the known megachiropteran faunas is more striking when one compares each island with adjacent islands. Two species on Vella Lavella occur also on Choiseul, which is about 35 miles northeastward, and two species occur also on Shortland, which is 120 miles northwestward (Fig. 16). Four of the five megachiropterans on Kolombangara also have been found on Choiseul, about 50 miles northward (Table 5). *Pteropus rayneri* is the only megachiropteran known from both Kolombangara and Vella Lavella, even though the islands are separated by only a few miles of water. Inadequate data possibly account for the differences in the megachiropteran fauna, but I suspect that some other factors are involved. Although Vella Lavella and Kolombangara do have one species (*P. rayneri*) in common, a different subspecies occurs on each island—*rubianus* on Kolombangara and *lavellanus* on Vella Lavella (Fig. 17 and Table 6). This indicates that some factor or factors are operating to keep megachiropterans from moving frequently or easily from one island to the other.

Each of several subspecies of species in the genus *Pteropus* are known from one or two small islands separated by only a few miles from other islands on which different subspecies occur (see Fig. 6). Judging from this kind of distribution, these bats do not move frequently from island to island. Possibly this is because they cannot easily cross water barriers, or are not inclined to do so because food is abundantly available throughout the year on their home

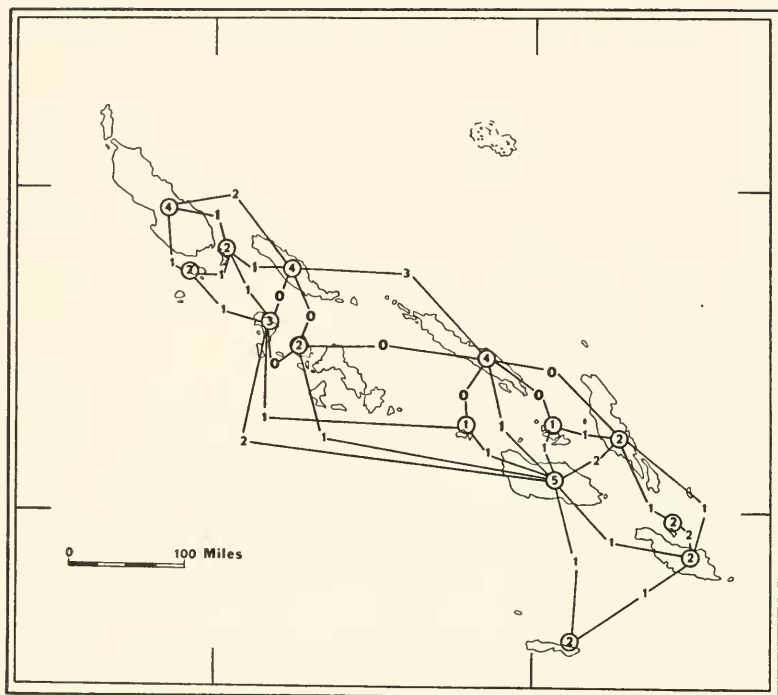


FIG. 17. The number of subspecies of megachiropterans known from individual islands (number within a circle) is compared with the number of subspecies common to different islands (number without a circle). For names of islands see Fig. 2.

island. Because "flying foxes" frequently are seen in flight over water several hundred yards from shore, the first factor probably is unimportant—at least where short distances are involved. It seems most likely that when abundant food is available these bats have no reason to move even moderate distances.

Distributions of subspecies of polytypic species are summarized in Table 6 and Figure 17. Generally, more subspecies are known from the larger islands than from the smaller islands (Guadalcanal with 5, Bougainville, Choiseul, and Santa Ysabel with 4, Fauro with 2.) The distributions of some subspecies can be used to judge the differential effectiveness of water gaps between islands. The distribution of *Pteropus rayneri lavellanus* and *P. rayneri rubianus* is an example.

Choiseul and Santa Ysabel are separated by about 50 miles of water (see Fig. 17) but have three subspecies in common (*Pteropus rayneri grandis*, *Dobsonia inermis minimus*, and *Nyctimene albi-*

venter minor.) Choiseul is about 50 miles from Kolombangara and about 35 miles from Vella Lavella, but shares no subspecies with these smaller islands although some species are shared (Tables 5 and 6). From these data one can conclude that exchange of genes between populations on Choiseul and populations on Santa Ysabel is frequent but for some reason exchange of genes between popu-

TABLE 6. A Summary of Distribution of Polytypic Species of Megachiropteran Bats in the Solomon Islands. Only Islands Well Known Faunistically Are Listed.

SUBSPECIES	Bougainville	Choiseul	Santa Ysabel	Nilai	Malaïta	Florida	Fauro	Shortland	Vella Lavella	Kolombangara	Russell	Guadalcanal	San Cristobal	Ugi	Rennell	Ontong Java
	<i>P. atrata atrata</i>	X	X													
<i>P. atrata anceps</i>			X									X				
<i>Pt. a. solomonis</i>												X				
<i>Pt. a. colonus</i>								X	X		X	X				
<i>Pt. a. grandis</i>				X												
<i>Pt. r. rayneri</i>					X							X				
<i>Pt. r. grandis</i>	X	X	X													
<i>Pt. r. rubianus</i>										X						
<i>Pt. r. lavellanus</i>									X							
<i>Pt. r. monoensis</i>																X
<i>Pt. r. cognatus</i>													X	X		
<i>Pt. r. rennelli</i>															X	X
<i>D. i. inermis</i>	X				X	X	X	X	X			X	X	X		
<i>D. i. minimus</i>		X	X													
<i>N. a. bougainville</i>	X									X						
<i>N. a. minor</i>		X	X				X				X					
Totals.....	4	4	4	1	2	1	2	2	3	2	1	5	2	2	2	1

lations on Vella Lavella and Choiseul and Kolombangara and Choiseul is infrequent. A series of small islands (Rob Roy, Wagina, and the Arnavon Islands, not named on the maps) connect Choiseul and Santa Ysabel in stepping-stone fashion (see Fig. 17). Possibly these small islands enhance movement of megachiropterans between Choiseul and Santa Ysabel.

Florida, of the Nggela Group, is approximately halfway between Santa Ysabel and Guadalcanal. *Pteralopex atrata anceps* occurs on Santa Ysabel and on Guadalcanal but is unknown from Florida. Fauro lies between Bougainville and Choiseul. *Pteralopex atrata atrata* and *Pteropus rayneri grandis* occur on Choiseul and on Bougainville but are unknown from Fauro. As suggested earlier, small islands like Fauro and Florida possibly cannot support large fruit bats, although they probably would utilize these small islands when in transit between larger islands.

Fauro apparently is important to the distribution of the two subspecies of *Dobsonia inermis* and *Nyctimene albiventer* in the Solomons (see Figs. 9 and 13). In both species, one subspecies is found in the eastern chain of islands and one subspecies is found in the western chain. Specimens of *Dobsonia inermis* from Fauro and Bougainville can be identified as the subspecies *inermis* whereas those from Choiseul are assignable to the subspecies *minusus*. *Nyctimene albiventer bougainville* occurs on Bougainville but specimens of *N. albiventer* from Fauro and Choiseul can be identified as the subspecies *minor*. Although interchange of genes occurs between populations on Bougainville and Fauro in the case of *D. inermis*, the population of *N. albiventer* on Fauro is at least partially isolated from the population on Bougainville.

Rennell and Ontong Java are relatively isolated from other islands in the Solomons (see Fig. 17). Only one kind of bat (*Pteropus howensis*) is known from Ontong Java and apparently is endemic to that atoll. *Pteropus tonganus geddiei*, one of the megachiropterans that occurs on Rennell (Table 5), also is found in the New Hebrides and on New Caledonia (Table 4). This makes *P. t. geddiei* the only megachiropteran bat in the Solomons that is more closely related to bats on islands to the southeast of the Solomons than to bats on other islands of the Solomons, the Bismarcks, or New Guinea, to the north and west. The other species of megachiropterans (*Dobsonia inermis* and *Pteropus rayneri*) on Rennell are found also on other islands in the Solomons. It is to be noted that Mayr (1931) regarded the avifauna of Rennell as most nearly like that of the New Hebrides and New Caledonia. He suggested that the prevailing winds from the southeast have been important for birds that have reached Rennell. The New Hebrides and New Caledonia are four and a half times farther from Rennell than are San Cristobal and Guadalcanal. On first consideration a person might doubt that the winds would be favorable enough to compensate for the great distance between Rennell and the New Hebrides and New Caledonia. Darlington (1938) has used the formula $X = n/m$ to obtain a comparison of barriers of different widths. [X = the probability of an individual crossing a barrier of width m ; the probability of an individual crossing a similar barrier of width n is the ratio n/m .] If this formula is applied here, one finds that winds from the southeast (that is, from the New Hebrides and New Caledonia) would have to be more than 100 times more

favorable than winds from the northeast (from Gaudalcanal and San Cristobal) in order to compensate for the distance of Rennell from the New Hebrides and New Caledonia. Even so, tropical storms with unusually strong winds, frequent during some parts of the year, possibly account for the present distributional pattern of bats and birds that live on Rennell.

Whatever the means by which bats of the species *P. tonganus* reached Rennell, the fact remains that specimens from Rennell cannot be distinguished from specimens of *P. tonganus geddiei* from the New Hebrides and New Caledonia, more than 500 miles to the southeast.

NOTE: An important and interesting paper on zoogeography of bats, which was published too late to be included here, is: Krzanowski, A., 1967, The magnitude of islands and the size of bats (Chiroptera), *Acta Zool. Cracoviensia*, 12:281-348.

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